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CHANGES IN LITTER INPUTS AND DECOMPOSITION IN HEADWATER STREAMS
DURING A MOUNTAIN PINE BEETLE INFESTATION OF WHITEBARK PINE

By

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B.A., Middlebury College, Middlebury, VT, 2006

Thesis

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ABSTRACT

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CHANGES IN LITTER INPUTS AND DECOMPOSITION IN HEADWATER STREAMS DURING A MOUNTAIN PINE BEETLE INFESTATION OF WHITEBARK PINE

Chairperson: Dr. Laurie B. Marczak

Headwater streams in forested landscapes are generally lacking in primary productivity and rely on allochthonous inputs to fuel secondary production. This close association with the forested landscape makes these streams sensitive to terrestrial disturbances. In the Greater Yellowstone Ecosystem (GYE) a climate change induced mountain pine beetle (*Dendroctonus ponderosae*, MPB) outbreak has been decimating whitebark pine (*Picea albicaulis*, WbP) forests over an extremely short time period. Among the possible implications of widespread WbP die-off, I predicted an increase in litter inputs to headwater streams and an increase in the quality (nitrogen content) of these litter inputs both of which would alter rates of organic matter processing and invertebrate communities in headwater streams. To test these predictions I quantified the mode of transport and rate of litter inputs to headwater streams in the GYE within ten streams distributed between two basins of differing levels WbP mortality and surveyed benthic invertebrate populations within those streams to determine whether MPB-mediated WbP mortality had an effect on detritivore communities. In addition, I carried out an experiment to compare differences in decomposition between needles from healthy WbP and those killed by MPB in a single stream within the high-mortality basin. Inputs of WbP needles were higher to streams in the basin with greater WbP mortality and these inputs were primarily entering streams via vertical transport. However, despite the increased quantity of inputs into these streams I found that invertebrate densities declined as WbP mortality increased. Furthermore, I discovered that naturally senescent needles from healthy trees decomposed faster than needles from MPB-killed trees despite higher nutrient levels in the MPB-altered needles. Although MPB attack does result in WbP litter with higher C:N than that which is associated with healthy trees, these needles may also contain elevated levels of defense compounds with insecticidal and anti-fungal properties. Further research is needed to determine whether possible MPB-induced increases in monoterpene concentrations affect needle decomposition. However, my results indicate that MPB infestations slow rates of nutrient processing in headwater streams despite an increase in litter quantity and quality.

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CHAPTER ONE: CHANGES IN ORGANIC MATTER INPUTS TO HEADWATER STREAMS FOLLOWING A MOUNTAIN PINE BEETLE INFESTATION OF WHITEBARK PINE.

INTRODUCTION

Streams are tightly coupled to the terrestrial landscapes through which they flow, particularly in forested headwaters. The forested riparian areas of headwater streams limit stream primary productivity through shading but simultaneously provide substantial inputs of organic material that fuel stream secondary production (Vannote et al. 1980). These allochthonous inputs of leaf litter, large wood, and dissolved nutrients dominate the resource base of most headwaters (Wallace et al. 1997), drive rates of secondary production (Tank et al. 2010) and determine aquatic food web structure (Marczak et al. 2007). Although often overlooked in management and conservation plans, headwater streams also transform and funnel vast quantities of terrestrial nutrients to downstream, frequently fish-bearing, reaches (Wipfli et al. 2007) aided by the processes of invertebrate and microbial driven decomposition (Greenwood et al. 2007).

The dependence of headwater stream function and productivity on terrestrial inputs suggests that large-scale basin disturbances have the potential to drive wholesale changes in stream food webs (Nakano et al. 1999, Kominoski et al. 2011). Disturbances that sufficiently alter the quality or quantity of organic matter inputs to streams could alter rates of organic matter processing, food web structure and species composition (Minshall et al. 1989, Minshall et al. 2001). Stream functional changes may ultimately propagate energy regime shifts back to riparian habitats or downstream to mainstem rivers and the communities that depend on them for ecosystem services and economic livelihoods (Wipfli et al. 2007).

Throughout the Rocky Mountain West, warmer temperatures are facilitating an outbreak of mountain pine beetle (*Dendroctonus ponderosae*, hereafter referred to as MPB) that is unprecedented in its areal extent and severity (Williams and Liebhold 2002, Kurz et al. 2008, Jewett et al. 2011). In the Greater Yellowstone Ecosystem (GYE) this outbreak has led to extensive mortality in whitebark pine (*Pinus albicaulis*, hereafter referred to as WbP), a signal of regional climate change that is on par with the melting of glaciers in the northern Continental Divide (Pederson et al. 2010).

In the GYE and across the West, researchers, managers, and the public have been focused on the terrestrial landscape when considering the implications of MPB infestation of WbP (Arno 1986, Ellison et al. 2005, Bentz and Schen-Langenheim 2006), particularly on the feedback of massive tree mortality for global climate cycles (Kurz et al. 2008), and the survival of charismatic species such as Clark's Nutcracker (*Nucifraga columbiana*, Tomback 2001) and grizzly bear (*Ursus arctos horribilis*, Logan 2006) across a wilderness landscape. However, changes in terrestrial ecosystem dynamics are only one likely outcome of this landscape scale disturbance.

In the current MPB outbreak, large swaths of forest have succumbed to beetles in a relatively short period of time, beginning in the mid-1990s (Aukema et al. 2006). Indeed, this appears to be the most extensive MPB outbreak ever recorded across all *Pinus* species (Logan et al. 2009, Jewett et al. 2011). There have been many studies on how watershed disturbances affect stream organic matter budgets, starting with Fisher and Likens (1972) and comprehensively documented by Webster and Meyer (1997), but no existing studies track the effects of MPB outbreaks on litter dynamics in streams. MPB infestations contribute a large pulse of litter to the forest floor (Klutsch et al. 2009)

and potentially into headwater streams. Trees begin to die within 2 weeks of a MPB attack and needles turn red within a year (Jewett et al. 2011). Red needles may remain on the tree for up to 5 years but the majority of needles are shed within 2-3 years following MPB infestation (Jewett et al. 2011). Previous research on MPB infestations in other *Pinus* species has shown a 40% increase in fine litter depth on the forest floor 4-7 years after MPB attack (Klutsch et al. 2009) and fine litter is significantly higher in forest stands with epidemic levels of MPB infestation versus those stands with baseline levels of infestation (Page and Jenkins 2007). It is likely that MPB infestations increase litter inputs into streams over a rapid timeframe either through direct litterfall or via lateral transport of accumulated litter from beneath affected stands, however, the magnitude of litter inputs and their dominant mode of transport to stream ecosystems have not been quantified.

Shifts in the quantity, quality or form of delivery of litter inputs have potentially large implications for stream energy budgets. Several studies have separately quantified the importance of vertical and lateral transport of detrital inputs to headwater streams (Winterbourn 1976, Webster et al. 1997, Colón-Gaud et al. 2008, Kanasashi and Hattori 2011). Litter can fall directly into streams from overhanging riparian vegetation, be transported downslope by water or gravity to enter the stream laterally, or be blown in by wind. Previous work has also shown that the quantity and mode of transport of litter inputs varies significantly throughout the year and is strongly influenced by storms (Colón-Gaud et al. 2008, Kanasashi and Hattori 2011). In general, vertical inputs are thought to be the dominant method of litter transport to headwater systems (Pozo et al. 1997). However, stream catchment terrain, particularly bank slope steepness, can increase

lateral transport (Kochi et al. 2004, Kanasashi and Hattori 2011) and in the few systems where lateral transport has been quantified, basin scale inputs have constituted between 10-30% of total inputs (Wallace et al. 1995, Kochi et al. 2004).

When considering allochthonous litter budgets for headwater streams it is also important to determine the length of time that litter is retained in the stream benthos because detritus must remain in place long enough to be processed by consumers if it is to contribute to a stream's energy budget (Jones 1997). The amount of time that litter is retained in streams is influenced by many factors, including hydrology (Tank et al. 2010, Imberger et al. 2011), channel geomorphology (Small et al. 2008), stream gradient (Webster et al. 1994), the presence of large woody debris (Jones 1997, Colón-Gaud et al. 2008), and the physical characteristics of the litter itself (Hoover et al. 2010).

To determine how MPB infestation of WbP may be altering energy budgets and nutrient cycling in stream catchments through changes in litter inputs, I examined the mode of input, quantity of inputs, and retention of WbP litter for 10 headwater streams with varying levels of stream catchment and basin-scale MPB infestation in the GYE. Within this study system I quantified and compared vertical and lateral WbP litter inputs, measured benthic retention of WbP needle litter for each stream, and examined the influence of basin characteristics and WbP mortality levels on litter input dynamics.

MATERIALS AND METHODS

Study sites

The study was conducted in 10 first-order streams within two basins in the Greater Yellowstone Ecosystem (Sheep basin, 42°02' N, 109°58' W, and Branham Lakes

basin, 45°31' N, 111°59' W, Figure 1-1). Both basins are characteristic of high-elevation temperate forests and are located in southwestern Montana, USA. Mean monthly air temperatures for Sheep basin range from -15 to 23° C and mean annual precipitation is averages 132 cm (<http://www.wcc.nrcs.usda.gov/snotel/Montana/montana.html>). Branham Lakes basin averages 103 cm of precipitation annually and mean monthly air temperatures range from -11 to 31° C. Whitebark pine dominates the forest canopy in both basins but other species present include subalpine fir (*Abies lasiocarpa*), and Englemann spruce (*Picea engelmannii*).

Basin and stream catchment characteristics

To determine whether beetle infestation increases the rate or pathway by which detritus enters stream systems, and to determine how variation in landscape characteristics affects them, I quantified vertical and lateral inputs of leaf litter in a single reach of 10 streams, 5 in each basin (Figure 1-2). These two basins represent two broad stages of beetle infestation in WbP – early infestation with low-mortality (Sheep), and peak to post-infestation with high-mortality (Branham Lakes). I selected 100-m reaches from streams that were as similar as possible in terms of size and physical parameters (Table 1-1); reaches usually began at the head of the stream. Among stream catchments, WbP mortality was variable: 1-7%% in the low-mortality basin and 22-94% in the high-mortality basin. Due to the pattern of MPB infestation it is generally not possible to intersperse study sites with different levels of infestation within a basin and thus it was necessary to use separate basins; streams within each basin were spatially auto-correlated with respect to large-scale patterns of WbP mortality. Due to this unavoidable

pseudoreplication, the inferences that can be drawn from the study are limited.

I quantified the percentage of WbP cover and mortality type at the basin and stream catchment scale. WbP percent cover in each basin was calculated after digitizing WbP cover, forested cover, and basin boundaries from Montana NAIP Color Orthophotos (NRIS 2011) in ArcMap 10.1 (ESRI 2011). Because WbP are interspersed with other canopy species, areas considered dominated by WbP did not contain exclusively WbP. The percentage of WbP cover for each stream catchment was visually estimated in the field from three high points in each basin.

Because tree canopy condition changes quickly during a MPB infestation I relied primarily on field observations to estimate mortality at each site. Mortality evaluations were based on visual observations and supported by comparison to the results described in Macfarlane et al. (2010). The proportion of WbP in green (healthy), red (killed by MPB but red needles remaining on trees), and gray stages (killed by MPB and no needles remaining) across basins and for each stream catchment was visually estimated from three points within each basin by two observers. Observations were made from high points within each basin so that it was possible to observe the entire area of interest. At each high point the entire basin was visible, however by combining observations from three different points and two observers I was able to better refine my estimations. To adjust these observations to reflect the relative proportion of canopy cover for green, red, or grey-stage WbP in each basin or stream catchment I divided mortality estimations by the percent WbP cover for each basin or stream catchment.

To characterize the overstory composition adjacent to each reach, I directed a laser pointer affixed to a level straight up from the center of the channel at 5-m intervals

throughout each reach and recorded which, if any, tree species it intersected (Elzinga 2001). The nearest distance between clusters (trees < 1 m apart) of one or more WbP and the stream was determined for all clusters along each focal reach (9-25 clusters per reach). Stream gradient was measured as the difference in elevation between the top and bottom of each 100-m study reach. I used a clinometer to measure slope angle on each side of the stream at the top, middle, and bottom of each reach and then averaged all values to obtain an average hillslope angle for each reach.

Mode of litter input

Mode of litter input was quantified using common designs for lateral and vertical litter traps (Elosegi and Pozo 2005). Vertical and lateral litter traps (10 of each) were installed at random intervals along each stream reach in early July 2012 and cleared monthly from late July 2012 to mid-October 2012. Lateral traps were constructed by stapling 1 m² of landscaping fabric to three wooden stakes. Lateral traps were placed with a 1-m opening perpendicular to and 0.5 m upslope from the stream bank and alternating sides of the stream where possible. Vertical traps consisted of a 0.5-m diameter wire hoop with an inset of loosely suspended mosquito netting mounted to a tripod of rebar and 9-gauge wire. Vertical traps were installed within the wetted area of study streams and their height was adjusted to be as close to the water surface during peak flow as possible.

Collected litter was sorted by type (WbP needles; WbP twigs, flowers, etc.; other conifer needles; other conifer twigs, flowers, etc.; other organic material), oven-dried (50° C for 48 h), and weighed to obtain dry mass (g). A 10% subsample of lateral trap

litter from each collection date was combusted at 500° C for 4 h to determine g ash-free dry mass (g AFDM) remaining. Litter AFDM was measured by subtracting ash mass from dry mass. These data were used to create a linear regression model for each litter category (Table 1-2). AFDM for the remaining lateral litter was determined by fitting dry mass for all samples to the linear model. Biomass values were pooled for each reach and used to extrapolate a reach-level estimate of vertical and lateral inputs for each stream, following methods outlined in Eloise and Pozo (2005).

Benthic retention

WbP detritus retained in streams was measured by placing a 0.5 x 0.5-m metal quadrat on 10 haphazard benthic locations within the wetted area of each reach and recording the percentage of visual cover of whitebark pine litter on June 26 and July 8, 2012 (high-mortality basin) and July 2, 2012 (low-mortality basin). These quadrat estimates were repeated at the middle of the study (August 15, 2012 for the low-mortality basin and August 20, 2012 for the high-mortality basin) and end of the study (October 3 and 4, 2012 for the high-mortality basin, October 5 and 6, 2012 for the low-mortality basin). During the final sampling period I collected all of the needles visible within a quadrat for three locations per stream after first estimating visual cover. Collected needles were oven-dried (50° C for 48 h) and weighed to obtain dry mass. These data were used to create a linear regression model to determine biomass relationships to the percentage of visual cover estimates (Table 1-2). Values from each quadrat were pooled and used to extrapolate a reach-level estimate of WbP detrital biomass and cover within each stream.

Drift entry and loss of WbP material

On each sampling date, drift nets were installed for 2 h above and below each study reach to determine rates of organic matter transports within each stream. I measured stream velocity using a Swoffer Instruments current meter (Seattle, WA, USA) along with stream width and depth in order to estimate discharge. Coarse particulate organic matter (CPOM) collected in the drift nets was sorted by type, oven-dried (50° C for 48 h), weighed to obtain dry mass, and combusted at 500°C for four hours. The g AFDM of CPOM collected was measured by subtracting ash mass from dry mass. Drift inputs and exports from the study reach were calculated following methods in Eloisegi and Pozo (2005). The volume of water filtered through each drift net was calculated by multiplying the area of water flowing through each net by average stream velocity. The concentration of CPOM in the drift was calculated by dividing the g AFDM of the collected drift sample by the filtered water volume. CPOM inputs and exports were then determined by multiplying CPOM concentration by stream discharge (stream area × velocity) and time between sample periods. Inputs of CPOM collected in the upstream nets were divided by the reach surface area and multiplied by 24 to determine the daily per meter contribution of CPOM from upstream to the study reach. The same calculations were followed to determine the daily per meter export of CPOM downstream from the study reach.

Statistical analyses

All analyses were performed in Program R (version 2.15.2, 2012-10-26) and JMP

(version 10, SAS 2012). Litter input and retention data were \log_{10} -transformed to meet normality assumptions prior to running statistical tests.

Quantity, transport mode, and retention of beetle-influenced WbP litter in streams

I used a fully crossed mixed-effects, nested ANCOVA to test whether WbP needle inputs differed by mode of input (vertical, lateral), basin, and sample date. In the model, transport mode and basin were fixed effects, sample period was a continuous covariate, and stream was a random effect nested within basin. I assessed differences in existing benthic retention of WbP needles using a fully crossed mixed-effects, nested ANCOVA where basin was a fixed effect, sampling period was a continuous covariate, and stream was a random factor nested within basin.

To determine the relationship between WbP needle inputs and retention of WbP litter within each stream I used a Welch two-sample t -test to compare inputs to benthic biomass. Drift sample data were used in conjunction with input and retention data to map an average reach-level energy budget for each basin.

Influence of basin and watershed characteristics

Basin characteristics (percentage of WbP cover; percentage WbP in green, red, or grey stage; hillslope; and stream gradient) were compared using separate Welch two sample t -tests followed by a Bonferroni correction.

I used principle components regression analysis to assess basin and stream level predictors of vertical, lateral, and total inputs as well as biomass retained in streams. The 10 independent variables were: (1) percent cover of WbP in each basin, (2) proportion of

green-stage WbP in each basin, (3) proportion of red-stage WbP in each basin, (4) proportion of grey-stage WbP in each basin, (5) percent cover of WbP in each stream catchment, (6) proportion of green-stage WbP in each stream catchment, (7) proportion of red-stage WbP in each stream catchment, (8) proportion of grey-stage WbP in each stream catchment, (9) average hillslope of the stream catchment, and (10) reach gradient.

Before running the analyses I tested for significant correlations among these variables and eliminated variables that were not likely to explain the data (variables 1, 2, 3, and 6 above). I eliminated the percent cover of WbP in each basin because I had intentionally selected basins with high levels of WbP percent cover. In addition, I eliminated the proportion of red-stage WbP in each basin because this did not differ between basins. I also eliminated the proportion of green-stage WbP in each basin and stream catchment because the proportion of red or grey-stage WbP explains this variable. I entered the remaining variables (variables 4, 5, 7, 8, 9, and 10 above) into a principle components analysis. I selected the principle components with eigenvectors greater than 1 (Fekedulegn et al. 2002) and regressed these values against the input data (daily vertical and lateral inputs and total biomass retained in streams) to determine how these landscape factors influence litter inputs and retention in streams. These variables cannot be separated because they are all highly correlated aspects of the same factor – the status of WbP on the landscape.

I used simple linear regressions to assess the relationship between PC1 and WbP litter inputs from other sources and benthic retention, at the stream catchment scale.

RESULTS

Basin and stream catchment characteristics

The percentage of WbP cover across the entirety of the low-mortality basin was 10%. The percentage of WbP cover in the high-mortality basin was 35% (Table 1-3). Although the high-mortality basin had a greater percent cover of WbP overall, WbP cover within stream catchments did not differ between basins. WbP cover across the 10 stream catchments ranged from 40-99% (Table 1-4). There was variation in the relative proportion of beetle-killed WbP (red and grey-phase trees combined), with significantly higher mortality in the high-mortality basin than in the low-mortality basin ($t_4 = 6.33$, $P = 0.02$).

Morphologically, the 10 stream reaches were generally alike (Table 1-3). Hillslope angle leading into each reach did not differ significantly between basins ($t_5 = 2.09$, $P = 0.72$, Figure 1-3) but was generally steeper for streams in the low-mortality basin versus those in high-mortality basin. There were no significant differences in reach gradient ($t_5 = 0.66$, $P = 1.00$), channel width ($t_7 = 2.01$, $P = 0.68$), and distance to WbP clumps ($t_4 = 1.55$, $P = 1.00$) between basins (Table 1-3).

Litter inputs

Overall litter inputs of all types were higher in the high-mortality basin ($F_{1,52} = 6.54$, $P = 0.01$, Figure 1-4 C) and arrived at streams within these basins in different ways (mode of transport \times basin, $F_{1,52} = 9.49$, $P = 0.003$); daily vertical inputs were greater for the high-mortality basin but daily lateral inputs did not differ between basins.

WbP needle inputs alone (as a subset of total inputs) also arrived at streams in different ways between the basins (mode of transport \times basin, $F_{1,52} = 6.40$, $P = 0.01$);

daily vertical inputs were significantly higher in the high-mortality basin ($P = 0.01$, Figure 1-4 A) but daily lateral inputs did not differ significantly between basins (Figure 1-4 B). Daily vertical inputs exceeded daily lateral inputs in the high-mortality basin ($P = 0.03$) but there were no differences between daily vertical and lateral inputs in the low-mortality basin ($P = 0.89$).

Principle components analysis loaded the relative proportion of grey WbP in the watershed, the percent cover of WbP in a catchment, the relative proportion of red WbP in a catchment, and the relative proportion of grey WbP in a catchment on the PC1 axis. This component accounted for 60% of the total variation in the data. Stream catchment hill slope angle and stream gradient were grouped on the PC2 axis, and the addition of this component explained 78% of the variability in the data (Table 1-5). PC1 was positively correlated with the relative proportion of grey WbP in a basin, the percent cover of WbP in a stream catchment, the relative proportion of red WbP in a stream catchment, and the relative proportion of grey WbP in a stream catchment. PC2 was strongly correlated with stream gradient.

PC1 significantly influenced daily vertical inputs of WbP needles ($F_{1,27} = 5.41$, $P = 0.03$). Neither PC1 or 2 was significant in regards to daily lateral inputs of WbP needles or the total biomass of WbP needles retained in streams.

At the stream catchment scale the quantity of WbP litter inputs is positively correlated with with PC1 components (Figure 1-5, $R^2 = 0.29$). The relationship between stream catchment level mortality in WbP and inputs of material from other sources is weaker (Figures 1-5), thus corroborating that the pattern in WbP inputs is attributable to WbP mortality and cover.

Benthic retention

Benthic coverage by WbP needles did not differ between basins or sample periods and there was no interaction between these variables. No explanatory variables met the $P = 0.05$ decision criteria for model inclusion in my model selection analysis. There was not a significant difference between the quantity of material entering the streams (vertical inputs) and benthic retention of litter. Likewise, the effect size of this difference was small (0.158) and there is no relationship between average biomass of WbP litter retained in streams and PC1 components (Figure 1-6, $R^2 = 0.01$).

WbP-specific contributions to organic matter budgets

I used input, retention, and drift data to graphically depict an average reach-level WbP needle budget for streams in each basin (Figure 1-7). There are clear differences between basins relating to the availability and transport of WbP needles in streams over the course of the study period. While these differences may be confounded by the greater basin-wide WbP cover in the high-mortality basin, WbP cover within stream stream catchments did not differ between basins. Over the course of the study, 79% [$\pm 11\%$] of WbP needle inputs to the streams in the high-mortality basin were vertical, 21% [$\pm 2\%$] of inputs were lateral, and 0.07% [$\pm 0.01\%$] of inputs entered study reaches via drift. However, for streams in the low-mortality basin only 30% [$\pm 3\%$] of inputs over the course of the study entered via vertical transport while lateral movement accounted for 70% [$\pm 3\%$] of total inputs. There were no drift inputs into low-mortality streams because these streams were either spring-fed or dry above the study reach.

DISCUSSION

This study is the first to document the relationship between MPB infestations of WbP and resulting changes in organic matter sources to headwater streams. My results indicate MPB-mediated WbP mortality, alongside WbP presence on the landscape, increase inputs of litter from WbP. Within individual stream catchments it is possible that WbP litter inputs increase following MPB infestation and that these inputs decline once trees have shed all or most of their needles. However, because mortality is confounded with percent cover of WbP, it is not possible to declare for certain that mortality, and not percent cover within stream catchments, is driving changes in litter inputs. Total inputs of WbP litter increased significantly with basin level mortality although this was driven primarily by the vast difference in vertical inputs.

Changes in litter inputs

Because my results are confounded by a lack of replication at the basin scale and spatial autocorrelation within the stream catchment scale, I cannot conclusively state that MPB infestation in WbP increases litter inputs to streams at the landscape scale over which the infestation occurs. However, my results demonstrate greater litter inputs in a basin with higher levels of MPB-caused WbP mortality as compared to one with little MPB-caused WbP mortality.

Vertical inputs were the dominant mode of transport for WbP needles and other litter into streams with high levels of catchment-level WbP mortality in this study. These

findings are in accord with other studies that have investigated litter transport into headwater streams (Pozo et al. 1997, Scarsbrook et al. 2001, Colón-Gaud et al. 2008). The overall dominance of vertical transport emphasizes the importance of streamside mortality when assessing how a MPB outbreak may change litter inputs to streams. Vertical inputs fall directly onto the stream surface; therefore trees must be near streams in order for this transport to occur. Thus, an increase in dead, red, trees within riparian areas will lead to greater needle inputs into headwater streams. However, an increase in red stage trees throughout the basin may not necessarily lead to more litter inputs if these trees are not near any streams. Therefore, when considering needle inputs into headwater streams and changes in stream organic matter budgets it may be more important to account for WbP mortality directly adjacent to streams rather than across an entire basin. Of course, landscapes with higher levels of overall mortality are likely to have more red-stage trees adjacent to streams, thus streams in a basin with greater mortality will likely receive elevated needle inputs as a consequence of this fact alone.

Although it is beyond the scope of this study, other researchers have noted that litterfall decreases with years since MPB infestation (Klutsch et al. 2009). After MPB attack, WbP and other *Pinus* species lose their needles. Once the needles are gone and the trees are grey there is no longer a source of needle litter remaining on the landscape and inputs to streams should subsequently decline or cease. This study, however, was not explicitly designed to examine inputs in a post-infestation (grey) context and thus none of the streams or basins examined had a substantial proportion of grey-phase trees. Additionally, grey-stage WbP was correlated with the other WbP cover and mortality factors included in my analysis.

MPB infestations send a large pulse of litter into headwater streams but this input is likely constrained to the first few years of beetle attack. Trees typically shed the majority of their needles within 5 years of attack and once the trees are grey they are no longer a source of vertical inputs. However, needles that have accumulated on the forest floor may continue to enter streams via lateral transport even after the trees are grey. Given the dominance of vertical inputs observed in this study, post-infestation lateral inputs would likely not be substantial enough to be considered a “pulse”. These lateral inputs, however, may resemble more of a “tail” that extends over a longer timeframe than the more substantive vertical contribution. Regardless of how long the tail of this pulse continues, it is probable that streams in post-infestation landscapes will exhibit organic matter dynamics that differ from both the pre-beetle and mid-infestation supply.

Although there was no significant difference in lateral inputs between basins, lateral inputs constituted a much higher percentage of total inputs in the low-mortality basin (70%) versus the high-mortality basin (21%). The relatively high percentage of lateral inputs across both basins, particularly in the low-mortality basin, is most probably due to variation in the steepness of stream catchments. Previous studies have shown that catchment hillslope angle is an important factor driving lateral inputs (Orndorff and Lang 1981, Kochi et al. 2010, Kanasashi and Hattori 2011, Hart et al. 2013). Hillslope angles for streams in the low-mortality basin were steeper than in the high-mortality basin, although the difference was not significant. Orndorff and Lang (1981) classified slopes greater than 30% as steep and found rapid litter movement on such slopes. Three of the 5 streams in the low-mortality basin had average hillslope angles that were greater than 30% whereas none of the streams in the high-mortality basin had hillslope angles greater

than 30%. The relatively steeper hillslopes in the low-mortality basin may be one reason that lateral transport comprised larger percentage of the inputs in this basin.

The relationship between MPB-mediated WbP mortality and changing litter inputs becomes clearer within, rather than across, landscapes. Although streams within each basin are spatially auto-correlated and mortality is correlated with percent cover, it appears that increased WbP mortality within individual stream catchments increases WbP litter inputs to associated streams. Although my study did not explicitly test this, it is likely that needle inputs would eventually decline as trees shift from red to grey. Thus, it is possible that MPB infestations produce a single relatively short-lived pulse of litter into streams that tracks the pace of the infestation itself.

Seasonality may have played a role in moderating differences in litter inputs and may explain why patterns I observed at the stream catchment level were not apparent at a larger, basin-wide, scale. Like all coniferous trees, the majority of needle-shed for healthy WbP occurs in the fall whereas beetle-killed trees generally begin to shed their needles within 12 months of attack and continue to shed needles throughout the year (Jewett et al. 2011). Because of time and access constraints I was only able to collect litter in August, September, and October – peak months for natural litterfall. Hart et al. (2013) found that lateral inputs exceeded vertical inputs in autumn, although this was primarily due to increases in deciduous litterfall. It is possible that natural, healthy, litterfall in the low-mortality basin, combined with steeper hillslope angles that promoted lateral over vertical transport, masked differences in litter inputs that would have been due to MPB-induced mortality alone.

In small streams, such as those in this study, litter retention is determined by both the characteristics of the bed surface and stream flow (Hoover et al. 2006). It appears that the capacity to retain litter material is comparable between streams in the two basins and that the majority of the needles entering streams in this study are remaining in the benthos for extended periods. Needles are not being immediately flushed from headwater systems, regardless of the level of WbP mortality. Thus this litter remains available to detritivores within the headwaters for potentially long periods of time. Benthic organic matter fuels secondary production and provides habitat for macroinvertebrates (Jones 1997). However, the “usefulness”, from an energy perspective, of detritus depends on how long it remains in the benthos.

Pine needles decompose slowly (Webster and Benfield 1986), thus it is important that they remain in the benthos for a long time if they are to contribute to the energy budget of streams in any meaningful way. In addition, litter only remains accessible to detrital consumers in the headwaters while entrained in the benthos. Finally, the longer detrital materials remain in the benthos the more likely they are to break down into smaller, more transportable, particles (Wotton 1994, Colón-Gaud et al. 2008). Although I found no relationship between the amount of WbP litter in the benthos and PC1 components, it is likely that benthic retention is driven more by factors such as channel geomorphology (Small et al. 2008) or hydrology (Tank et al. 2010).

My results indicate that MPB outbreaks increase WbP litter inputs to and thus alter organic matter budgets within streams and that the relative amounts of WbP on the landscape together with the extent of WbP mortality are related to increasing litter inputs. Thus, organic matter budgets for streams in catchments dominated by WbP are likely to

change drastically over the course of a MPB outbreak. I found that significantly more needles fell into streams in the high-mortality basin, however, a much larger proportion of needles remained in streams within the low-mortality basin (80% versus 47%) although the total amount of detrital material did not differ between basins. This difference is almost certainly not due to WbP mortality but may be because 2 out of 5 of the low-mortality streams were dry by the end of the study period and thus had dramatically reduced capacity to transport litter over the course of the study. Likewise, the low-mortality streams that retained surface flow throughout the study period were generally smaller than the streams in the high-mortality basin. However, given that flows increase drastically with snowmelt, springtime floods likely flush a large pulse of detritus out of these systems.

Confounding interactions between local scales and outbreak dynamics

The large-scale pattern of MPB infestation across the West suggests that ecological questions related to this disturbance should be addressed at a similarly broad scale. Thus, in this study I first examined my data at a landscape-level scale by comparing differences in inputs between 2 basins with differing levels of WbP mortality. However, because like most disturbances, MPB outbreaks are patchy, I also examined my data at a finer scale by comparing differences in inputs across all streams regardless of basin.

The inferences that can be drawn from this study are limited by lack of replication at the largest basin-scale and spatial autocorrelation in outbreak dynamics at the stream catchment scale. However, these are problems that are commonly encountered in

landscape ecology (Lichstein et al. 2002). Spatial autocorrelation is particularly problematic as auto-correlated pseudoreplicates violate the independence assumptions of many statistical tests and may bias the results of logistic regression models (Nielson et al. 2002). Jelinski and Wu (1996) demonstrated that autocorrelation decreases at larger scales, however, it is not always possible to work at scales large enough to overcome this issue. Oftentimes replication is limited in studies that examine large landscapes (Turner 2005), and this lack of replication may confound results.

My large-scale analysis is confounded by basin-level differences that may influence litter inputs. For example, the relative steepness of hillslopes in the low-mortality basin may facilitate greater lateral transport than the generally less steep stream catchments in the high-mortality basin. Likewise, my fine-grain analysis may be biased because streams within a basin are spatially auto-correlated. However, both levels of analysis show a positive correlation between WbP litter inputs to streams and PC1 factors – mortality, and stream catchment cover. In addition, given that previous studies have shown substantial increases in litterfall to forest soils following MPB infestation across many forest types (Page and Jenkins 2007, Klutsch et al. 2009, Keville 2011), the results of this study are likely broadly applicable to forests affected by MPB.

Conclusion

In this study I documented that MPB infestations in WbP increase litter inputs into mountain streams although this finding is confounded by a correlation between WbP mortality and percent cover. The greater the percent cover of WbP on the landscape, the more likely it is that there will be MPB-killed WbP. However, my findings are in line

with what was expected given previous research on terrestrial litter dynamics following MPB outbreaks (Page and Jenkins 2007, Klutsch et al. 2009) as well as general investigations of litter inputs into headwater streams (Winterbourn 1976, Pozo et al. 1997). In addition, I found that much of the WbP litter entering streams remains in headwaters, at least during the summer and fall. These findings have important implications for understanding organic matter budgets in headwater streams over the course of a MPB infestation. Managers who are concerned about changes in allochthonous inputs to such streams should monitor the health of trees nearest to streams in order to stay abreast of shifting organic matter dynamics in these systems. Likewise, if protective measures are to be implemented in a basin it would be most beneficial to treat WbP nearest streams in order to mitigate the effects of MPB infestations on aquatic systems.

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TABLES

Table 1-1. Physical parameters of each study stream with standard deviation reported where appropriate. There are not significant differences in the physical parameters of these streams but stream catchment mortality is significantly different between basins.

Basin	Stream	Aspect	Reach length	Reach gradient (m/km)	Average hill slope	Average channel width (m)	Average wetted width (m, late June)	Average depth (m, late June)	Catchment mortality (red and grey stage)
Branham Lakes (high mortality)	1	East	100m	2.3	29 ± 7%	1.84 ± 0.49	1.80 ± 0.76	0.22 ± 0.07	94%
	2	West	100m	1.1	13 ± 7%	3.29 ± 1.61	1.51 ± 0.79	0.21 ± 0.08	22%
	3	Southwest	100m	2.1	20 ± 10%	3.00 ± 2.23	1.79 ± 0.93	0.17 ± 0.04	86%
	4	Southwest	100m	2.3	17 ± 6%	1.59 ± 0.53	0.94 ± 0.38	0.12 ± 0.04	86%
	5	Southwest	100m	1.1	18 ± 18%	1.27 ± 0.49	1.21 ± 0.80	0.1 ± 0.03	37%
Sheep Creek (low mortality)	1	Southwest	100m	0.7	18 ± 9%	0.47 ± 0.26	0.32 ± 0.11	0.04 ± 0.03	1%
	2	Southwest	100m	5.2	23 ± 16%	0.92 ± 0.66	0.38 ± 0.18	0.06 ± 0.02	1%
	3	Southwest	100m	1.5	57 ± 10%	2.56 ± 1.08	1.74 ± 0.91	0.07 ± 0.03	5%
	4	Southwest	100m	4.5	35 ± 13%	1.90 ± 0.65	1.03 ± 0.30	0.05 ± 0.02	7%
	5	Southwest	100m	0.4	41 ± 15%	1.05 ± 0.27	0.66 ± 0.16	0.06 ± 0.02	2%

Table 1-2. Regression equations for calculating AFDM or biomass of litter. AFDM equations were used to calculate AFDM of collected litter from dry mass based on a 10% subsample. The detrital biomass equation was used to calculate dry biomass of WbP needles based on the percent cover of such detritus within a 0.25-m² benthic quadrant.

	Regression	<i>P</i> value	R²
WbP needles AFDM	0.955 + 0.0067x	< 0.001	0.9984
WbP twigs, flowers, etc. AFDM	0.943 + 0.0010x	< 0.001	0.9979
Other conifer needles AFDM	0.932 + 0.0007x	< 0.001	0.9998
Other conifer twigs, flowers, etc. AFDM	0.943 + 0.0002x	< 0.001	0.9983
Other organic material AFDM	0.405 + 0.04714x	< 0.001	0.6451
Percent benthic cover to biomass	0.134 + 4.761x	< 0.001	0.698

Table 1-3. Whitebark pine cover and mortality in focal basins. Branham Lakes basin has high levels of WbP mortality and Sheep Creek basin has a relatively healthy WbP population.

Basin	% WbP cover in basin	% WbP in basin that is healthy	% "red" WbP in basin	% "grey" WbP in basin
Branham Lakes	35%	50%	30%	20%
Sheep	19%	65%	25%	10%

Table 1-4. Whitebark pine cover and mortality in stream catchments. WbP in Branham Lakes basin is largely dead due to MPB and WbP in Sheep Creek basin is relatively healthy overall.

Basin	Stream	% WbP cover in stream catchment	% healthy WbP in stream catchment	% "red" WbP in stream catchment	% "grey" WbP in stream catchment
Branham Lakes (high mortality)	Branham Lakes 1	99%	30%	20%	50%
	Branham Lakes 2	55%	60%	25%	15%
	Branham Lakes 3	95%	10%	30%	60%
	Branham Lakes 4	95%	10%	60%	30%
	Branham Lakes 5	68%	45%	50%	5%
Sheep Creek (low mortality)	Sheep 1	45%	98%	0%	2%
	Sheep 2	40%	97%	0%	3%
	Sheep 3	50%	90%	5%	5%
	Sheep 4	65%	89%	1%	10%
	Sheep 5	55%	97%	1%	2%

Table 1-5. Factor loadings for the first two principal components derived from the analysis of watershed and stream catchment characteristics of the 10 first-order study streams. Percentage of the total variance explained by each of these principal components is provided in the bottom row.

Factor	PC1	PC2
Relative proportion of grey WbP in a basin	0.923	-0.223
Percent cover of WbP in a stream catchment	0.926	0.211
Relative proportion of red WbP in a stream catchment	0.934	-0.020
Relative proportion of grey WbP in a stream catchment	0.848	0.301
Stream catchment slope	-0.520	0.253
Stream gradient	-0.105	0.907
Percentage of total variance explained	59.8	77.6

FIGURES



Figure 1-1. Location of study sites within the northern portion of the Greater Yellowstone Ecosystem. Branham Lakes basin is in the Tobacco Roots mountains and has some of the highest levels of WbP mortality for the GYE. Sheep Creek basin is in the Absaroka mountains and contains one of the healthiest remaining populations of WbP in the GYE.

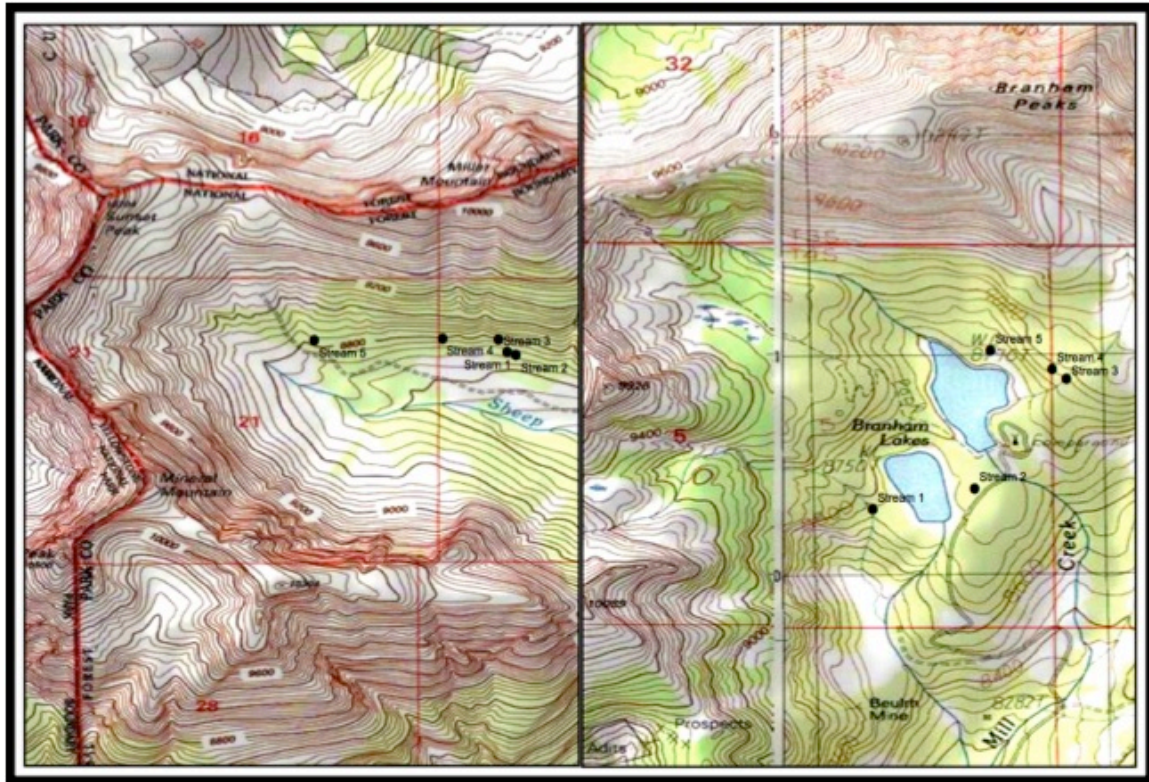


Figure 1-2. Focal streams for whitebark pine litter input study in Sheep Creek (left) and Branham Lakes (right) basins. Most of the WbP in Sheep Creek basin are healthy but Branham Lakes basin has experienced severe WbP mortality due to MPB.

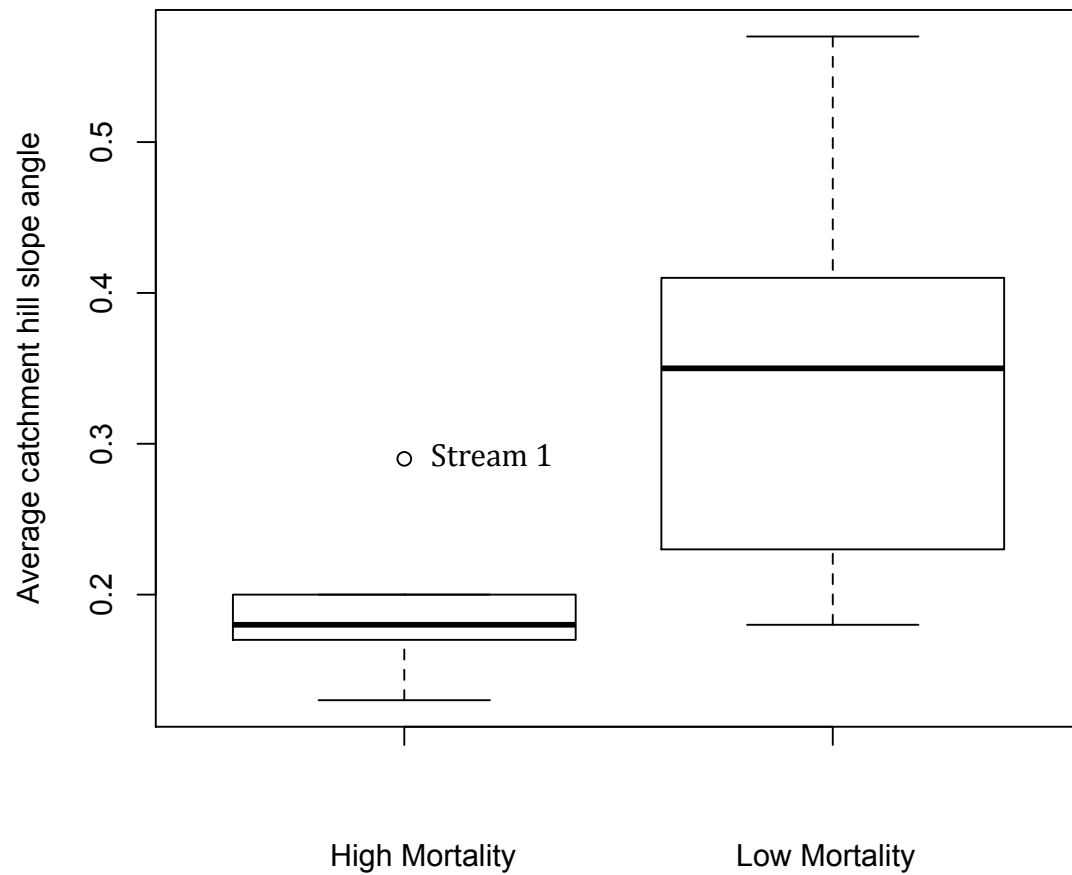


Figure 1-3. Stream catchment hillslope angle for streams in high and low-mortality basins. There is not a statistically significant difference in hillslope angle between basins.

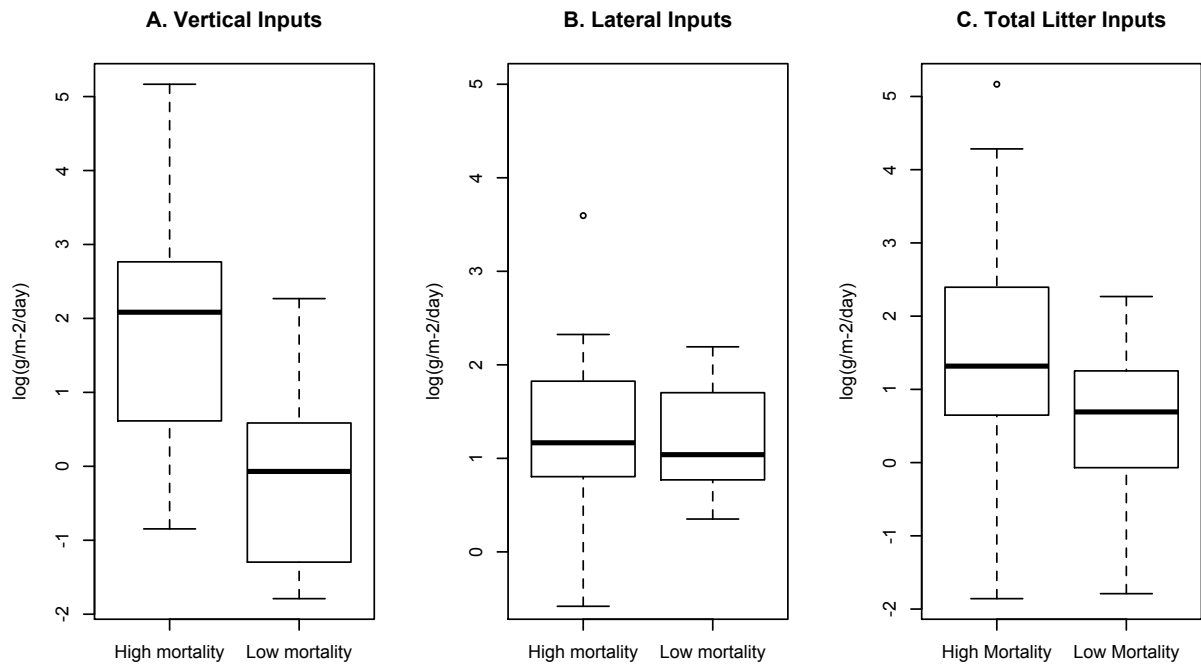


Figure 1-4. A) Differences in total vertical inputs ($\log(g/m^2/day)$) to streams between basins, averaged across all sample periods. The difference is statistically significant. B) Differences in total lateral inputs ($\log(g/m^2/day)$) to streams between basins, averaged across all sample periods. C) Differences in total litter inputs ($\log(g/m^2/day)$) to streams, averaged across all sample periods.

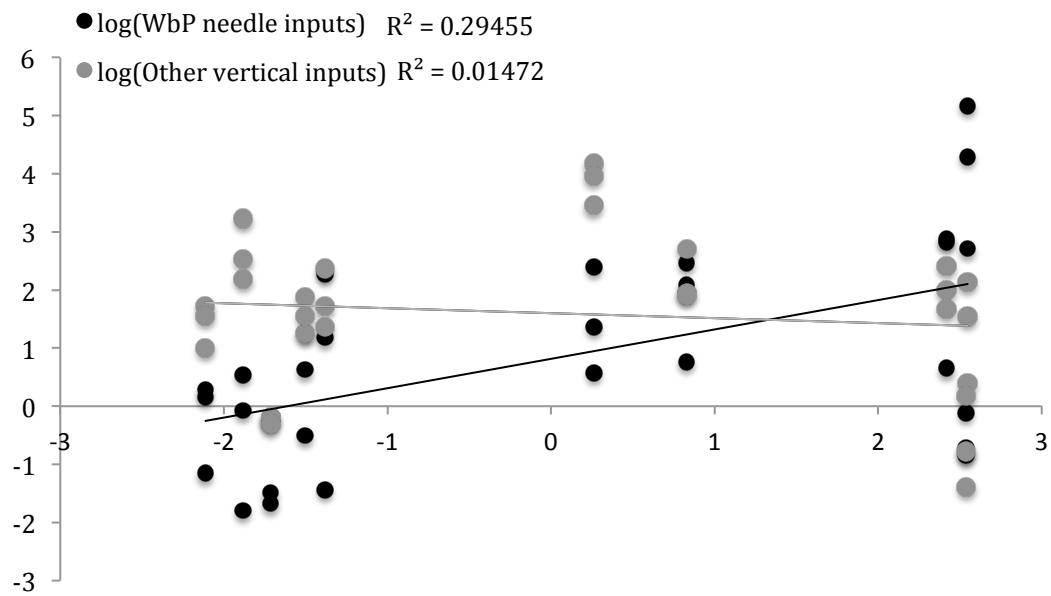


Figure 1-5. Vertical WbP needle inputs have a positive relationship with PC1 components (grey-stage WbP in a basin, percent cover of WbP in a stream catchment, red-stage WbP in a stream catchment, and grey-stage WbP in a stream catchment). Vertical inputs from other sources are not related to PC1 components.

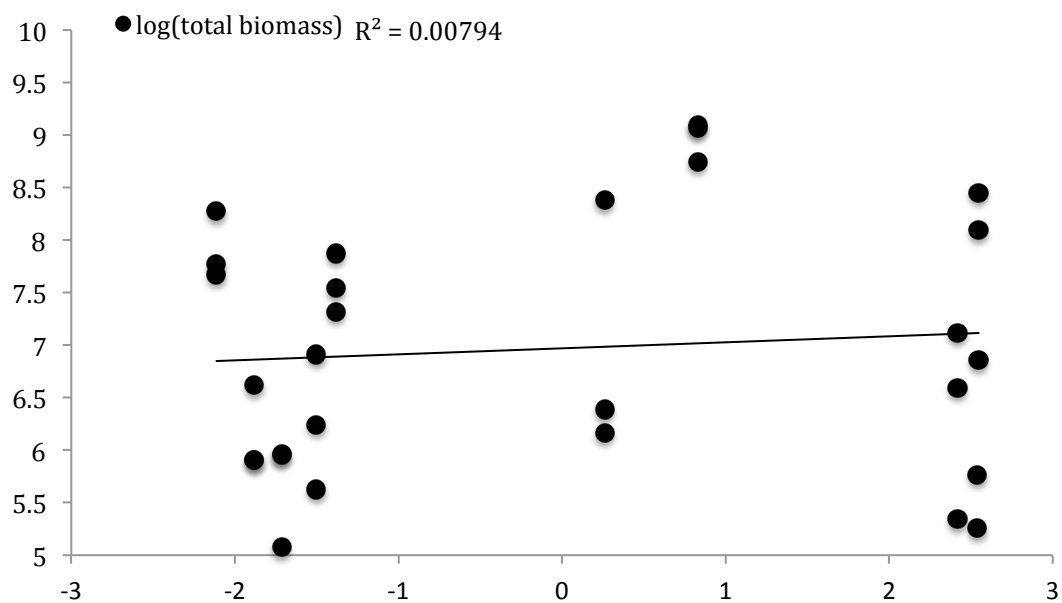


Figure 1-6. There is no relationship between WbP litter retained within a stream and PC1 components (grey-stage WbP in a basin, percent cover of WbP in a stream catchment, red-stage WbP in a stream catchment, and grey-stage WbP in a stream catchment).

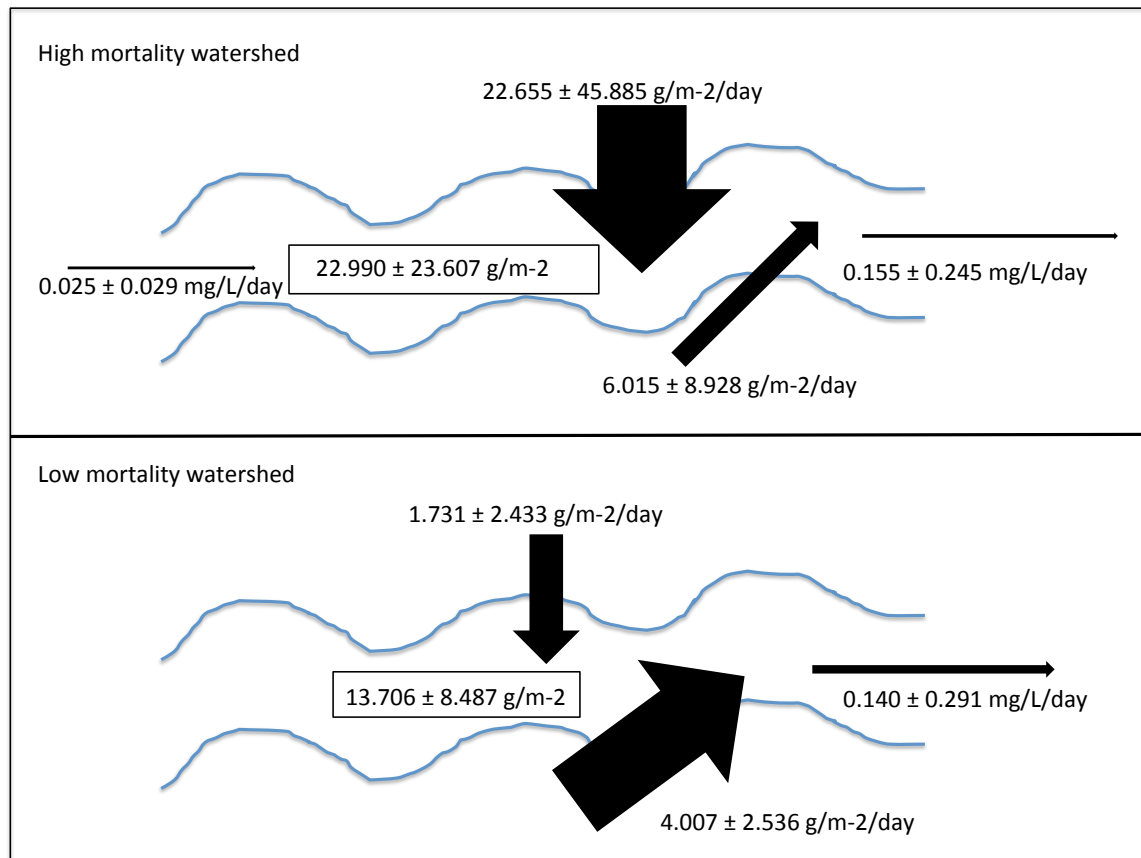


Figure 1-7. Reach-level whitebark pine needle budgets for an average stream in low and high-mortality basins in this study. Arrows are scaled to represent the proportion of total litter entering the study reach. Values within boxes in each stream represent amount of whitebark pine needles retained in the benthos. Values were obtained by averaging data across all sample dates for 5 focal streams in each basin and are reported as the mean ± one standard deviation.

CHAPTER TWO: CHANGES IN AQUATIC DECOMPOSITION FOLLOWING A MOUNTAIN PINE BEETLE INFESTATION OF WHITEBARK PINE

INTRODUCTION

The quantity and quality of resources available in ecosystems are key factors that determine the abundance and spatial distribution of organisms, which in turn govern ecosystem processes. Litter inputs to streams in conifer-dominated systems are generally low quality relative to consumer requirements (high C:N ratios) and consequently decompose slowly (Johansson 1995, Murphy and Giller 2000), leading to slower rates of nutrient cycling than are found in systems with higher quality litter inputs (Webster and Benfield 1986). However, headwater streams in forested landscapes rely on allochthonous inputs for secondary production (Vannote et al. 1980) and streams in coniferous forests receive significantly fewer litter inputs than those flowing through deciduous forests (Hart et al. 2013) increasing the likelihood that consumers in these systems are food limited (Richardson 1991). Thus, an increase in the quality and quantity of litter inputs to headwater streams in coniferous-dominated stream catchments may have strong effects on ecosystem processes.

Experimental manipulations of litter quantity in streamside channels (Rowe and Richardson 2001) and in natural streams (Reice 1991, Tiegs et al. 2008) have shown that litter shredding invertebrates can track litter resource patches in streams. Such resource tracking can lead to aggregations of shredders on leaf packs and subsequently accelerate decomposition (Rowe and Richardson 2001). Comparable results have been found in experimentally resource-depleted streams that drain clear-cut stream catchments (Benfield et al. 2001). In these and similar situations where litter resources in streams are patchy or scarce, aggregations of shredders on experimental leaf packs can be massive

and accelerate decomposition beyond the rates caused by microbial activity alone (Robinson et al. 1998, Baldy et al. 2007). In addition, because aquatic insects seek out resources and respond to new inputs, changes in streamside vegetation or litter inputs can have subsequent effects on food webs (Melody and Richardson 2004, Yoshimura 2012).

Leaves from various tree and shrub species decay at different rates (Webster and Benfield 1986) and support different microbial (Ostrofsky 1997) and invertebrate community assemblages (Cummins et al. 1989, Graça 2001). Differences in decomposition rates between litter species are largely determined by the physical and chemical qualities of the litter itself (Hauer and Lamberti 2007) as well as differences among streams (Robinson et al. 2000). These differences in leaf characteristics have been found to account for the majority of variation in decomposition rates between species (Ostrofsky 1997, LeRoy and Marks 2006), to influence food quality for detritivores (Graça 2001), and to influence the abundance and composition of macroinvertebrates associated with leaf litter (Richardson et al. 2004, LeRoy and Marks 2006).

In contrast, comparatively little is known about how variation in litter quality *within* a species affects ecosystem processes and nutrient cycling. A notable exception is the work of LeRoy and colleagues (2007) which demonstrated that genetic variation within a tree species (oaks and cottonwoods) affects leaf carbon to nitrogen (C:N) ratios which in turn affects ecosystem processes including decomposition and nutrient cycling in both forests and their associated streams. In their study as much as 72% of the variation in stream litter decomposition rate in these species was explained by litter genotype (and associated variability in litter quality). Additional sources of within-

species variation in litter quality and decomposition within streams, such as the changes wrought by terrestrial herbivory, have yet to be fully explored.

Insect herbivores demonstrably alter soil and surface water inorganic N concentrations, particularly when populations achieve outbreak proportions (Morehouse et al. 2008). Huber (2005) found elevated nitrate (NO_3^-) concentrations in seepage water following a bark beetle outbreak – these levels peaked 5-years post-outbreak and were still measurable after 7 years. This high N soil water has the potential to reach stream ecosystems. Increases in stream NO_3^- concentrations have been documented in a Japanese red pine ecosystem following a pine wilt disease epidemic (Tokuchi et al. 2004) and increases in stream nutrient loads following insect outbreaks (Swank et al. 1981, Webb et al. 1995, Pitman et al. 2010) and forest harvesting (Neary et al. 2009, Spoelstra et al. 2010) are a common response to forest disturbance. These terrestrially driven changes in stream water chemistry are known to alter the abundance and community composition of both microbial communities and benthic invertebrates (Benfield et al. 2001) and in so doing alter rates of litter decomposition (Baldy et al. 2007). The direct effects of herbivory-induced changes in leaf litter chemistry on rates of decomposition (both terrestrial and aquatic) have received comparably little attention (Gandhi and Herms 2010). However, previous research has demonstrated that disturbances that alter leaf biogeochemistry, such as herbivory, can affect litter decomposition (Findlay and Jones 1990, Findlay et al. 1996).

Rates of microbial processing of terrestrial detritus in streams are partly determined by background nutrient levels in streamwater (Grattan and Suberkropp 2001, Rosemond et al. 2002). Under nutrient-rich conditions, leaf litter decomposition rates in

streams increase, primarily via enhanced microbial activity resulting from a nutrient-mediated increase in the proportion of litter carbon that is accessible to the microbial community (Gulis and Suberkropp 2003). For example, Stelzer and colleagues (2003) used experimental additions of N and P in a temperate hardwood forest stream to show that dissolved nutrients had strong positive effects on microbial respiration and biomass, indicating nutrient limitation. Microbially mediated increases in detrital quality may lead to an increase in both C and N flow to consumers that extends to multiple trophic levels; however, enrichment may equally promote C loss from systems via increased respiration and export of particulate C (Benstead et al. 2009), with corresponding implications for larger scale cycling of nutrients.

In the Greater Yellowstone Ecosystem (GYE) an unprecedented outbreak of mountain pine beetle (*Dendroctonus ponderosae*, hereafter referred to as MPB) has severely affected whitebark pine (*Picea albicaulis*, hereafter referred to as WbP) (Williams and Liebhold 2002, Kurz et al. 2008, Jewett et al. 2011). This outbreak has led to widespread mortality of WbP throughout the GYE (Macfarlane et al. 2010), resulting in a number of repercussions for ecosystem function in high-elevation forests (Ellison et al. 2005, Logan 2006, Logan et al. 2010, Kegley 2011).

MPB effects on WbP include the loss of needles from affected trees beginning the first year after infestation (Jewett et al. 2011) and a change in the quality of the needles that are shed (Morehouse et al. 2008). In MPB-infested stands, trees drop their needles before N resorption occurs, resulting in a large pulse of litter to the forest floor with lower C:N ratios than typical coniferous material (Morehouse et al. 2008). In ponderosa pine (*Pinus ponderosa*), bark beetle outbreaks typically induce this high-N needlefall

pulse within 2 years of the outbreak, driving shifts in soil N cycling between infested and uninfested stands (Morehouse et al. 2008). In other coniferous forest ecosystems affected by herbivorous insect outbreaks this pulse of higher quality leaf litter appears to be driving shifts in functions such as rates of litter decomposition in soils and associated shifts in larger scale cycling of C and N (Chapman et al. 2003, Morehouse et al. 2008).

Although there is little in the literature discussing the impacts of landscape scale terrestrial insect defoliation events on stream macroinvertebrates, examining the effects of other terrestrial disturbances may help us to predict how MPB infestations might affect aquatic communities. Following the loss of riparian vegetation, headwater streams can shift from being heterotrophic to being dominated by autotrophic production.

Disturbances that decrease riparian vegetation, such as fire, typically favor scraper invertebrates over shredders because of associated declines in allochthonous inputs and increases in primary productivity (Minshall et al. 1989). Meanwhile, disturbances that increase allochthonous inputs, such as logging, generally lead to at least short-term increases in shredders and collectors (Stone and Wallace 1998). Given these patterns it is likely that MPB infestations may temporarily increase allochthonous inputs in the short term, favoring shredders. However, the simultaneous decrease in canopy cover that occurs when trees lose their foliage may favor shredders and collectors initially with a shift towards scraper dominance after the initial pulse of inputs has passed.

Because of these previously observed differences in litter quality for both herbivore-affected pine needles in general and WbP litter in particular, I predicted that WbP litter from MPB-killed trees that has entered aquatic habitats would decompose faster than litter from healthy WbP. I hypothesized that this accelerated rate of

decomposition would be due to two factors: (1) microbial processing should be higher for MPB-altered litter and as a result shredders should aggregate on these needles, and (2) invertebrates, particularly shredders, would be more abundant in watersheds with high levels of MPB infestation of WbP. To test these hypotheses and determine how MPB infestations alter nutrient cycling in streams flowing through WbP-dominated stream catchments, I compared in-stream decomposition rates of shed needles from healthy and MPB-altered WbP. In addition, I surveyed benthic macroinvertebrates in basins with high and low levels of MPB infestation to assess whether this terrestrial disturbance has altered decomposer assemblages within streams that flow through affected stream catchments. As MPB infestations and other forest pathogen outbreaks continue to spread across forested landscapes such assessments can provide insights into how these landscape-level changes may alter ecosystem function at multiple levels and across ecosystem boundaries.

MATERIALS AND METHODS

The intent of this study was to use decomposition of both healthy and MPB-altered needles in streams that were located in a comparatively healthy forest and a comparatively heavily MPB-infested forest with high WbP mortality. The experiment within the healthy forest was designed to capture the initial responses of the stream community to the potential litter pulse and the experiment within the forest with high WbP mortality was designed to capture ways in which decomposition might differ when the stream community has already adjusted to changes in litter dynamics. Two streams (one from each of these basin types) were selected for decomposition studies. In order to

provide background information on the stream decomposer community across these basin types, we surveyed 6 streams in each basin to characterize the invertebrate community. Although these streams were nested within a high or low-mortality basin, at the individual stream catchment level there was variability in the extent of WbP mortality. We categorized this variation by the percent of WbP in a stream catchment that was red or grey and used these mortality estimates to compare invertebrate communities across a gradient of beetle-influence.

Study sites

The study was conducted in two watersheds within the Greater Yellowstone Ecosystem (Sheep basin, 42°02' N, 109°58' W, and Branham Lakes basin, 45°31' N, 111°59' W; Figure 2-1). These two basins characterize two stages of MPB infestation in WbP – early infestation, relatively healthy (Sheep), and peak to post-infestation with high-mortality (Branham Lakes) (Macfarlane et al. 2010). Because this type of infestation moves as a synchronized “front,” interspersing infested and healthy study sites is generally not possible (Aukema et al. 2006). Mean monthly air temperatures for Sheep basin range from -15 to 23° C and mean annual precipitation averages 132 cm (<http://www.wcc.nrcs.usda.gov/snotel/Montana/montana.html>). Branham Lakes basin averages 103 cm of precipitation annually and mean monthly air temperatures range from -11 to 31° C. The overstory canopy in both basins is dominated by whitebark pine (*Pinus albicaulus*) but also include subalpine fir (*Abies lasiocarpa*) and Engleman spruce (*Picea engelmannii*).

Litter decomposition

P. albicaulis needles were collected from five trees throughout each study site in April 2012. Needles were collected from beetle-killed trees by shooting small branches from the overstory with a shotgun and obtained from live trees by shaking the tree and collecting dropped needles or removing dead needles from living trees by hand. Litter was air-dried for 1 month prior to use. Five grams of needles were weighed and placed in 33 x 5.08-cm PVC cylinders (details of construction in Kominoski et al. (2011)). Each cylinder was fitted with fine-gauge mesh (0.48 mm opening size) at the upstream and downstream ends. Mesh size was large enough to allow water to flow freely through the cylinders but did not allow the loss of needle fragments. Eight 12.5-mm² holes were drilled haphazardly around the upstream half of the cylinders to allow invertebrate colonization. Holes were sized and positioned to minimize the chance that needles would drift out of the containers. Additional needle decomposition cylinders without holes restricted invertebrate access to measure microbe-specific effects on decomposition.

I deployed 168 needle decomposition cylinders into Sheep Creek (in the low-mortality basin, hereafter referred to as the low-mortality stream) on 5 July 2012 and 168 cylinders into Mill Creek (in the high-mortality basin, hereafter referred to as the high-mortality stream) on 10 July 2012 (Figure 2-2). These two (second-order) streams were chosen for this experiment as each was the largest stream in each basin that flowed through WbP. I placed 42 of each of the following types of cylinders into both streams: MPB-altered needles exposed to microbial and invertebrates consumers (MPB-I), MPB-altered needles with invertebrate consumers excluded (MPB-M), needles from healthy trees exposed to microbial and invertebrate consumers (G-I), and needles from healthy

trees with invertebrates excluded (G-M). Empty cylinders with invertebrate entrance holes were placed in each stream to estimate (and subsequently correct for) organic matter passively entering cylinders during the study. Six cylinders of each type were removed from the stream after 3 hours to estimate handling loss and initial needle chemistry. Needles were removed from each cylinder, placed in individual plastic bags, and frozen for transport back to the laboratory.

Unfortunately, water levels in the low-mortality stream fell precipitously following the start of the experiment and had dried completely after three sample dates, halfway through the study. Prior to flow ceasing, water levels in the stream dropped sufficiently for many of the decomposition chambers to be either not fully submerged or to have very little water flowing through them. This limits the confidence that can be placed on those results and eliminates the potential to draw comparisons between rates of decomposition between high-mortality and comparatively healthy conditions. Here I present the values calculated in the low-mortality stream for illustrative purposes and caution that these results have been strongly influenced by the shortness of the hydroperiod.

Litter cylinders were removed from the stream after 14, 28, 42, 56, 70, and 84 days of incubation (14, 28, and 42 for the low-mortality stream). While this experiment was of shorter duration than other conifer decomposition studies (Robinson et al. 2000, Collen et al. 2004), access and temperature constraints in this high-elevation system limited the duration of the experiment. Litter was rinsed from each cylinder into clear plastic bins to separate invertebrates from litter and to wash away sediment. Litter was

subsequently hand-collected with forceps, placed in plastic bags, frozen and returned to the laboratory for processing.

Litter chemistry and mass loss

All of the litter material from each sample date was oven-dried at 50° C for two days. Subsamples from three of each type of cylinder per sample date were ground with a Wiley Mill (20-mesh screen), weighed into tin capsules (~4 mg each), and combusted on a CHNS-O elemental analyzer (CE Instruments EA 1110, Thermo Fisher, USA) for total litter C and N (Environmental Biogeochemistry Laboratory, University of Montana). The remaining ground subsamples were analyzed for P content using ICP analysis at the Colorado State University Soils, Water, and Plant Testing Lab (Fort Collins, CO). Samples for each litter type were pooled by needle type and collection date and used to determine variation in litter quality by needle type during the process of microbial and invertebrate dominated decomposition.

Total oven-dried mass for the remaining three cylinders of each type per sample date was measured after oven drying. A 33% subsample of litter from each collection date was combusted at 500 °C for 4 h to estimate ash-free dry mass (g AFDM) remaining. Litter AFDM was measured by subtracting ash mass from dry mass. These data were used to create a linear regression model, ($y = 0.9028x + 0.2731$, $r^2 = 0.9558$, $P < 0.001$); AFDM for the remaining containers was determined by fitting dry mass to the model. The percent litter mass remaining over time was subsequently fitted to a negative exponential model, $Mt = M_0e^{-kt}$, where M_0 is initial mass and Mt is the mass of the litter at each time t (Petersen and Cummins 1974) to determine the decomposition rate, k , for

each treatment.

Microbial respiration

Microbial respiration was determined in the field by measuring the oxygen (O_2) uptake of decomposing leaf material at stream water temperatures following methods described by Gulis and Suberkropp (2003). On each collection date 10 needles from three litter containers per needle type were placed in respiration chambers containing 25 mL of stream water and placed in the stream. Oxygen concentrations (mg/L) were recorded every 5 min with a YSI 85 Dissolved Oxygen Meter (Yellow Springs, OH, U.S.A.) for 30 min in darkness. Three additional chambers containing only stream water served as controls. Oxygen consumption was determined from the slope of the regression of oxygen concentration over time minus the control slope (determined from stream water alone). This preliminary statistic was scaled up from 10 needles per half hour to be expressed as oxygen consumption per g AFDM per hour by multiplying by twice the inverse of the average mass of 10 WbP needles (~ 0.156 g), or 12.78 (Gulis and Suberkropp 2003).

Stream water chemistry

Water chemistry data were collected in order to assess factors beyond the experimental treatments that influence litter decomposition in each study stream. On each sampling date stream temperature and dissolved oxygen were measured using a YSI 85 Dissolved Oxygen Meter (Yellow Springs, OH, USA). Stream pH was measured with an Oakton pH Tester 10 (Vernon Hills, IL, USA). Three replicate 60 mL filtered water samples were collected on each sampling date and kept frozen for analysis. Water

samples were analyzed for nitrate, ammonium, and soluble reactive phosphorus at the Montana Environmental Lab (Kalispell, MT) using a Lachat Quick Chem 8000 segmented flow analyzer. However, because the low-mortality stream dried halfway through the study I was unable to relate water chemistry parameters to differences in decomposition. Therefore, water chemistry comparisons between the two study sites are presented for illustrative purposes only and to facilitate comparisons with other locations.

Benthic macroinvertebrate survey

To assess whether benthic invertebrate communities varied in conjunction with MPB infestation of WbP I surveyed benthic invertebrate composition within six first- or second-order streams in each watershed, or 12 streams total (Figure 2-2). Streams ($n = 10$) were chosen because they were the same streams used in the litter input study (Chapter 1) or were the same streams ($n = 2$) in which the decomposition portion of this study occurred. Benthic invertebrates were collected using a Surber sampler in 10 haphazardly sited locations along a 100-m reach of each stream; Surber samples were a minimum of 1 m apart. Invertebrates were removed from the Surber net and immediately stored in 95% ethanol. Individuals were later counted, identified to the lowest possible taxonomic level (except Chironimidae and Oligochaeta which were determined to the level of genus and class respectively), and assigned to a functional feeding group (Merritt and Cummins 1996, Wallace et al. 1999). Invertebrate identification and classification was performed by taxonomic experts from Rhithron Associates Inc. (Missoula, MT).

Statistical analyses

Statistical analyses were performed in Program R (version 2.15.2, 2012-10-26) and PC-ORD (version 6). Where assumptions of normality were not met and could not be achieved through transformation, data were analyzed with Wilcoxon rank-sum tests. Prior to running statistical analyses I removed large outliers ($n = 8$). For decomposition data these outliers were identified using box and whisker plots. These data likely represented containers that lost needles during transport to the field site or through the holes I had drilled for invertebrate access. For microbial respiration data these outliers ($n = 79$) resulted from instrument malfunction. Because of variable sample sizes and differences in data reliability, I conducted separate analyses for each stream.

To assess changes in litter biomass over the course of the experiment I calculated daily decomposition rates and a decay constant (k) for each treatment. I then assessed changes in g AFDM, needle quality (C:N ratio and phosphorus levels), and rates of microbial respiration by treatment over time using separate ANCOVA models. For each model, needle type and decomposer were fixed factors, and time (days in stream) was a continuous covariate. All interactions were included in the models. Microbial respiration served as a proxy for microbial colonization of needles in this experiment (Gulis and Suberkropp 2003). Differences in water chemistry between the two streams in this study were compared using a MANOVA with all field-measured parameters (temperature, pH, dissolved oxygen, ammonia, total nitrates, and orthophosphate levels) as response variables followed by Tukey's HSD post-hoc tests.

Finally, to determine whether MPB infestation of WbP altered aquatic invertebrate community composition, I examined differences in components of diversity for invertebrate taxa between basins. To determine whether taxa differed more between

basins than within basins I compared beta diversity (Bray-Curtis) using an analysis of similarities (ANOSIM) followed by a principal components analysis for graphical display of patterns. Then, to compare mean variance in invertebrate taxa between sites I used separate Wilcoxon rank-sum tests to compare differences in mean alpha diversity (Shannon-Wiener index), overall species richness, mean taxa richness, and functional feeding groups between basins. To determine which taxa had significant affinities for each basin I used an indicator taxa analysis following methods in Dufrene and Legendre (1997). Finally, I calculated simple linear regressions to assess changes in invertebrate densities in streams in relation to WbP mortality in associated stream catchments.

RESULTS

Mass Loss

In the high-mortality stream the fastest rate of decomposition was observed for needles from healthy trees in the presence of invertebrates ($0.034 \pm 0.018 \text{ g day}^{-1}$; Table 2-1) while the slowest rate of decomposition occurred for MPB-influenced needles decomposing with microbes only ($0.026 \pm 0.008 \text{ g day}^{-1}$; Table 2-1). The decay rates (k) in this stream ranged from 0.008 ± 0.004 (healthy needles in the presence of invertebrates) to 0.006 ± 0.002 (MPB-influenced or healthy needles decomposing with microbes only) (Table 2-1). Overall, needles from healthy trees decomposed faster than MPB-altered needles ($F_{1, 80} = 5.30$, $P = 0.02$, Figure 2-3 A) and needles exposed to invertebrate consumers lost more mass regardless of needle type, although this trend was not significant (Figure 2-3 B). Within the shorter hydroperiod of the low-mortality stream

the overall rate of decomposition was faster for needles exposed to invertebrate consumers than when invertebrates were excluded (decomposer treatment x days in stream, $F_{1,46} = 4.53$, $P = 0.04$; Table 2-2 C).

Needle nutrients

At the high-mortality site needles from healthy trees had significantly higher initial C:N values than needles from MPB-infested trees ($t_{2,69} = 6.61$, $P = 0.001$, Figure 2-4 A). During decomposition, needle C:N decreased over time from 53.3 ± 3 to 38.2 ± 2.7 (healthy needles) and 50.4 ± 1.2 to 37.5 ± 1.6 (MPB-altered needles) but there were no differences in the rate of this loss between treatment types (Table 2-3 A). In the high-mortality stream, phosphorus levels decreased more over time for needles accessible to invertebrate consumers (decomposer x days in stream, $F_{1,60} = 4.82$, $P = 0.03$, Table 2-4 A, Figure 2-5). I was unable to test total phosphorus levels for pre-treatment needles, but on day 14 there was no significant difference in total phosphorus between needle types at either site (Figure 2-4 C and D).

Initial values of C:N between needle types at the low-mortality site did not differ ($t_{2,66} = 1.43$, $P = 0.26$, Figure 2-4 B) but C:N declined significantly faster for MPB-altered needles (Table 2-3 B). Neither decomposer nor needle type influenced rates of phosphorus loss from needles in the low-mortality stream (Table 2-4 B).

Microbial respiration

In the high-mortality stream, rates of microbial respiration did not differ by needle type or consumer identity (Table 2-5 A) and respiration was highly variable on all sample

days. In the low-mortality stream needles in microbial decomposition chambers had greater respiration than needles with invertebrate decomposers and needles from healthy trees had greater respiration than needles from beetle-killed trees (needle type x decomposer x days in stream, $F_{1,16} = 12.22$, $P = 0.003$, Table 2-5 B).

Stream chemistry

Water chemistry parameters across all sample dates were significantly different between the high and low-mortality streams (Pillai's Trace = .0989, $F_{6,12} = 179.15$, $P < 0.001$). Tukey's HSD post-hoc tests indicated that the low-mortality stream had a lower mean temperature ($P < 0.001$, Figure 2-6 A), and higher pH ($P < 0.001$, Figure 2-6 B), dissolved oxygen ($P < 0.001$, Figure 2-6 C), orthophosphate levels ($P = 0.01$, Figure 2-6 D), and total nitrates ($P < 0.001$, Figure 2-6 E) compared to the high-mortality stream. Levels of ammonia did not differ between these sites ($P = 0.64$, Figure 2-6 F).

Benthic macroinvertebrates

Beta diversity (turnover) differed between the high and low-mortality basins (ANOSIM, $R = 0.1938$, $P = 0.001$, Figure 2-7). However, there were no differences in mean alpha diversity ($W = 1390$, $P = 0.49$), overall species richness ($W = 1240$, $P = 0.11$), or mean taxa richness ($W = 1240$, $P = 0.11$) between basins.

Relative abundances by functional feeding groups differed between the high and low-mortality basins. Collector-gatherers were significantly more abundant in the high-mortality watershed ($W = 1914$, $P = 0.007$, Figure 2-8 A); numbers of collector-filterers ($W = 1870$, $P = 0.008$, Figure 2-8 B) and scrapers ($W = 1836.5$, $P = 0.02$, Figure 2-8 C)

were significantly higher in streams in the low-mortality basin. Shredders ($W = 1311.5$, $P = 0.23$, Figure 2-8 D), omnivores ($W = 1238.5$, $P = 0.08$, Figure 2-8 E), and predators ($W = 1465.5$, $P = 0.82$, Figure 2-8 F) did not differ between basins.

The indicator species analysis confirmed that the collector-filterers are significantly affiliated with the low-mortality stream ($IV = 35.6$, $P = 0.03$). No other functional feeding group was significantly affiliated with either basin. The taxon with the highest overall indicator value was a collector-gatherer, *Baetis bicaudatus*, which was strongly affiliated with streams in the low-mortality basin ($IV = 48.3$, $P < 0.001$). The second highest indicator value (for *Megarcys sp.*, a predator), had an indicator value of 37.3, $P < 0.001$ and was also associated with the low-mortality basin. Significant indicator taxa are show in Table 2-6. At the stream catchment scale (individual streams within basins), invertebrate densities decreased as WbP mortality increased when measured by the proportion of both red-phase ($R^2 = 0.28$) and grey-phase WbP ($R^2 = 0.31$) in the stream stream catchment. This pattern held for all feeding groups, including shredders (Figure 2-9 A and B).

DISCUSSION

This study is the first to document changes in an important ecosystem function in aquatic systems following landscape scale MPB infestations in a terrestrial ecosystem. Contrary to expectation, needles from healthy trees decayed faster than MPB-altered needles despite being lower in initial quality, as defined by the C:N ratio. Thus, at the same time as they cause a decrease in the C:N ratio of litter entering streams, MPB infestations may decrease the palatability of allochthonous inputs. Although the

mechanisms behind this change in palatability remain speculative, differences in needle palatability may explain why invertebrate population densities also decreased with increasing WbP mortality in stream catchments, despite the pulsed increase in litter inputs. Overall, these results indicate that outbreaks of terrestrial herbivorous insects have the potential to slow nutrient processing in headwater streams.

Influence of beetle-induced nutrient change on litter decomposition

Overall, pine needles decayed slowly and at rates similar to those observed in elsewhere. In this study k for WbP needles decomposing in a stream already heavily influenced by beetle infestation was 0.006– 0.008. In comparison, other studies have reported pine needle k values ranging from 0.0030 – 0.0038 (Short et al. 1980) to 0.0054– 0.0093 (Whiles and Wallace 1997). There was too much variation in my microbial respiration data to compare these rates with those observed in other studies.

It is well documented that decomposition rates are influenced by litter quality (Webster and Benfield 1986, Couteaux et al. 1995, Ostrofsky 1997) and that variation in leaf nutrient levels may explain differences in decomposition even within a single species (LeRoy et al. 2007). These studies demonstrate that higher quality litter, i.e. that with a lower C:N, decomposes faster. Indeed, litter quality is often the driving factor behind decomposition rates (Webster and Benfield 1986, LeRoy and Marks 2006). Like other researchers (Morehouse et al. 2008, Keville 2011), I found MPB-altered needles to have a significantly lower C:N ratio than litter from healthy trees and there was a corresponding difference in the rates at which these needles decomposed in the stream system. However, contrary to my hypothesis, needles from healthy trees decomposed faster than

needles from beetle-killed trees despite MPB-altered needles being higher in initial quality.

There are several hypotheses that may explain why the MPB-altered needles decomposed more slowly. The most likely explanation for these results is that needles from beetle-killed trees decomposed slower because of additional chemical compounds induced by herbivory. When conifers are attacked by an insect herbivore they employ a number of defenses including chemical responses. Following attack by many different species of bark beetles, monoterpene concentrations in conifers increase (Raffa and Smalley 1995). Of note was that MPB attack led to an increase in monoterpene concentrations in jack pine (*Pinus banksiana*) needles (Erbilgin and Colgan (2012). Monoterpenes are a class of chemicals that help plants, particularly conifers, to resist herbivory (White 1994, Litvak and Monson 1998). At high doses monoterpenes are lethal to insects and can inhibit microbial activity (Langenheim 1994, Raffa and Smalley 1995, Hwang and Kim 2002). These compounds are highly resilient and do not decrease in concentration after needle senescence (White 1991, Wilt et al. 1993). Because of this resilience researchers have proposed that monoterpenes and other secondary chemicals may inhibit decomposer organisms for many years after senescence (Kainulainen and Holopainen 2002). It is likely that needles from MPB-killed trees have higher concentrations of monoterpenes which may in turn slow microbial activity and deter macroinvertebrate consumers.

One alternative hypothesis that may explain why the MPB-influenced needles decomposed more slowly is that leaching rates were faster for these needles and the resulting shift in litter quality led to the observed differences in decomposition. My

results show that litter C:N declined rapidly over time, particularly for the needles from healthy trees, such that by the end of the study litter C:N was lower in these needles. However, this shift in litter quality did not mirror observed patterns in decomposition, as the needles from healthy trees decomposed faster on all sampling dates but litter quality did not shift until later in the study. Additionally, because litter C:N declined over time for both needle types this change in quality is likely due to microbial colonization of the litter more so than leaching. Indeed, it is possible that litter quality increased faster for needles from healthy trees because increased concentrations of secondary chemicals in the MPB-altered needles inhibited microbial colonization of these needles.

It is also possible, although unlikely, that genetic variation in the needle litter led to differences in decomposition. Genetic variation within a species has been shown to affect rates of litter decomposition (Schweitzer et al. 2005, LeRoy et al. 2007). While I attempted to ensure that the samples used for C:N analysis reflected a diverse composite of litter from the decomposition experiment, only a very small (4 mg) amount of material was analyzed in each sample. Therefore, it is possible that a smaller number of trees were represented in the C:N analysis than in the decomposition experiment and that the individuals tested for litter C:N were not representative of the sample population as a whole.

Benthic invertebrate responses to basin-level mortality and organic input quality

I expected that shredder densities would be higher in the high-mortality basin if invertebrates were responding to the increase in inputs of higher-quality litter. Contrary to my hypothesis, however, the relative abundance of shredders did not differ by basin

level mortality. However, there were significant differences in abundance for other feeding groups between streams in low and high-mortality sites. The site with a healthier forest overstory had higher numbers of collector-filterers and scrapers while the site with high overstory mortality had significantly more collector-gatherers. Given that these feeding groups, particularly scrapers, are associated with high primary productivity and that these study streams were characterized by fairly open overstories, it is possible that primary productivity and not litter inputs is the main resource driving productivity in these systems.

The observed differences between invertebrate abundance in streams within the high and low-mortality basins do not appear to be related to WbP mortality as a main driver. Rather, differences in invertebrate communities may be related to water temperature (streams in the low-mortality basin were colder), permanence (2 of the 5 streams surveyed in the low-mortality basin stopped flowing mid-summer), or habitat structure. The main difference between invertebrate communities in high and low-mortality streams was the abundance of collector-gatherers. Invertebrates in this group feed on detritus that is on or within sediment on the stream bottom. This group is known to respond positively to disturbances that increase coarse particulate organic matter (CPOM) in streams (Gurtz and Wallace 1984, Brown et al. 1997). However, scrapers, which were more abundant in the low-mortality streams, also tend to increase after disturbances with population shifts that mirror that of collector-gatherers (Gurtz and Wallace 1984). Collector-filterers, which were significantly affiliated with the low-mortality stream, feed on the same food resource as gatherers but have similar habitat requirements to scrapers (Whiles and Wallace 1997). Therefore, it is likely that habitat, specifically benthic

structure, is the most likely variable to explain differences in collector-gatherer, collector-filterer, and scraper abundances between basins.

Although there were no patterns linking changes in invertebrate communities to WbP mortality at the basin scale, invertebrate densities within streams decreased with increasing WbP mortality in associated stream catchments. In the previous chapter I documented an increase in (presumably MPB-altered) WbP needle inputs to streams with increasing WbP mortality. Given that increased resources tend to support greater secondary productivity, I had hypothesized that this increase in inputs would lead to increases in invertebrate populations. However, my results indicate that MPB attack likely changes needle chemistry in such a way as to inhibit decomposition. Therefore, although more needles are entering streams in MPB-infested stands, this litter is processed more slowly. In turn, it appears that these reduced rates of organic matter processing may be limiting secondary productivity within affected streams. As with observed differences in invertebrate abundances between basins, differences in densities are confounded with chemical and habitat differences between streams in the two basins and it is thus impossible to isolate the effects of WbP mortality. However, given the observed changes in decomposition for MPB-altered needles, and the role that litter decomposition plays in driving secondary productivity in headwater streams, it is likely that changes in WbP litter inputs is influencing these observed differences in invertebrate densities.

CONCLUSIONS

Contrary to what was expected, needles from healthy trees decayed faster than MPB-altered needles despite having higher C:N ratios. Decomposition rates for pine needles are generally low as this litter is high in refractory compounds that make feeding difficult for invertebrates (Graça 2001). Therefore, it is possible that benthic invertebrates avoid feeding on pine needles regardless of litter biogeochemistry. However, chemical changes that occur in WbP needles in response to MPB attack may further deter decomposers from feeding on these needles. Due to the possible effects of increased monoterpene concentrations on decomposition, future research should quantify MPB-induced monoterpene concentrations in needles and more thoroughly investigate whether these chemicals inhibit detritivore consumption of needles.

Given that decomposition is slower for MPB-altered needles it is likely that rates of nutrient processing are lower in streams with high levels of MPB-killed WbP and thus fewer nutrients are available to support secondary productivity. Thus, MPB-affected streams may support lower densities of invertebrate consumers. This is supported by my results, which show a decrease in invertebrate densities associated with increasing WbP mortality. These results indicate that in-stream productivity may decrease following MPB infestation of surrounding forests.

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TABLES

Table 2-1. Needle nutrient levels, daily mass loss rates, and k values for each treatment. Values are reported as the mean \pm SD.

Stream	Decomposer	Needle Source	Preliminary C:N	Day 14 total P (mg/kg)	Decomposition rate (g/day ⁻¹)	k
Mill	Invertebrate + Microbial	Healthy tree	55.02 \pm 1.09	1102.6 \pm 74.17	0.034 \pm 0.018	0.008 \pm 0.004
Mill	Microbial	Healthy tree	55.02 \pm 1.09	1102.6 \pm 74.17	0.028 \pm 0.009	0.006 \pm 0.002
Mill	Invertebrate + Microbial	MPB-altered	50.51 \pm 0.46	1164.67 \pm 67.99	0.029 \pm 0.010	0.007 \pm 0.002
Mill	Microbial	MPB-altered	50.51 \pm 0.46	1164.67 \pm 67.99	0.026 \pm 0.008	0.006 \pm 0.002
Sheep	Invertebrate + Microbial	Healthy tree	53.27 \pm 3.13	1112.6 \pm 116.17	0.022 \pm 0.014	0.005 \pm 0.003
Sheep	Microbial	Healthy tree	53.27 \pm 3.13	1112.6 \pm 116.17	0.016 \pm 0.007	0.003 \pm 0.002
Sheep	Invertebrate + Microbial	MPB-altered	50.47 \pm 1.29	1223.33 \pm 74.17	0.021 \pm 0.009	0.005 \pm 0.002
Sheep	Microbial	MPB-altered	50.47 \pm 1.29	1223.33 \pm 74.17	0.016 \pm 0.006	0.003 \pm 0.001

Table 2-2: ANOVA tables for factors influencing needle decomposition in A) the high-mortality stream, B) the high-mortality stream with outlier treatment-day removed, and C) the low-mortality stream.

A. High-mortality	DF	Sum Sq	Mean Sq	F value	P value
Days	1	22.846	22.486	640.823	< 0.001
Needle Type	1	0.102	0.102	2.868	0.094
Decomposer	1	0.132	0.132	3.703	0.058
Days x Needle Type	1	0.001	0.001	0.034	0.854
Days x Decomposer	1	0.025	0.025	0.688	0.409
Needle Type x Decomposer	1	0	0	0	0.988
Days x Needle Type x Decomposer	1	0.017	0.017	0.485	0.486
Residuals	83	2.959	0.036		

B. High-mortality, excluding MPB-I day 70	DF	Sum Sq	Mean Sq	F value	P value
Days	1	20.699	20.699	614.014	< 0.001
Needle Type	1	0.179	0.179	5.3	0.024
Decomposer	1	0.069	0.069	2.054	0.156
Days x Needle Type	1	0.025	0.025	0.751	0.389
Days x Decomposer	1	0.003	0.003	0.074	0.787
Needle Type x Decomposer	1	0.009	0.009	0.273	0.603
Days x Needle Type x Decomposer	1	0	0	0.008	0.928
Residuals	80	0.27	0.034		

Low-mortality	DF	Sum Sq	Mean Sq	F value	P value
Days	1	0.729	0.729	37.994	< 0.001
Needle Type	1	0.003	0.003	0.116	0.695
Decomposer	1	0.123	0.122	6.394	0.015
Days x Needle Type	1	0.015	0.015	0.782	0.381
Days x Decomposer	1	0.087	0.087	4.533	0.039
Needle Type x Decomposer	1	0	0	0.015	0.903
Days x Needle Type x Decomposer	1	0	0	0	0.987
Residuals	46	0.883	0.019		

Table 2-3: ANOVA tables for factors influencing needle C:N during decomposition in A) the high-mortality stream, and B) the low-mortality stream

A. High-mortality	DF	Sum Sq	Mean Sq	F value	P value
Days	1	2497.990	2497.990	277.876	< 0.001
Needle Type	1	12.760	12.760	1.419	0.237
Decomposer	1	1.130	1.130	0.126	0.724
Days x Needle Type	1	20.620	20.620	2.294	0.134
Days x Decomposer	1	2.790	2.790	0.310	0.579
Needle Type x Decomposer	1	9.720	9.720	1.082	0.302
Days x Needle Type x Decomposer	1	9.550	9.550	1.063	0.306
Residuals	73	656.240	8.990		

B. Low-mortality	DF	Sum Sq	Mean Sq	F value	P value
Days	1	87.870	87.870	13.254	< 0.001
Needle Type	1	346.370	346.370	52.243	< 0.001
Decomposer	1	1.800	1.800	0.282	0.605
Days x Needle Type	1	16.730	16.730	2.523	0.120
Days x Decomposer	1	3.260	3.260	0.491	0.487
Needle Type x Decomposer	1	9.080	9.080	1.370	0.249
Days x Needle Type x Decomposer	1	6.320	6.320	0.953	0.335
Residuals	40	265.190	6.630		

Table 2-4: ANOVA tables for factors influencing total phosphorus content in needles during decomposition in A) the high-mortality stream, and B) the low-mortality stream

A. High-mortality	DF	Sum Sq	Mean Sq	F value	P value
Days	1	287,805	287,805	36.996	< 0.001
Needle Type	1	57	57	0.007	0.932
Decomposer	1	38,400	38,400	4.936	0.030
Days x Needle Type	1	25,059	25,059	3.221	0.078
Days x Decomposer	1	37,488	37,488	4.819	0.032
Needle Type x Decomposer	1	13,590	13,590	1.747	0.191
Days x Needle Type x Decomposer	1	634	634	0.082	0.776
Residuals	60	466,768	7,779		

B. Low-mortality	DF	Sum Sq	Mean Sq	F value	P value
Days	1	31,214	31,213.6	3.444	0.074
Needle Type	1	12,484	12,484.2	1.378	0.251
Decomposer	1	1,028	1,027.8	0.113	0.739
Days x Needle Type	1	14,698	14,698.2	1.622	0.214
Days x Decomposer	1	3,259	3,259.2	0.360	0.554
Needle Type x Decomposer	1	648	648.2	0.072	0.791
Days x Needle Type x Decomposer	1	20,409	20,408.7	2.252	0.145
Residuals	27	244,702	9,063.0		

Table 2-5: ANOVA tables for factors influencing microbial respiration on needles during decomposition in A) the high-mortality stream, and B) the low-mortality stream

A. High-mortality	DF	Sum Sq	Mean Sq	F value	P value
Days	1	0.003	0.003	0.087	0.769
Needle Type	1	0.026	0.003	0.073	0.789
Decomposer	1	0.025	0.025	0.703	0.405
Days x Needle Type	1	0.017	0.017	0.480	0.491
Days x Decomposer	1	0.013	0.013	0.362	0.550
Needle Type x Decomposer	1	0.025	0.025	0.703	0.405
Days x Needle Type x Decomposer	1	0.014	0.014	0.399	0.530
Residuals	60	2.150	0.036		

B. Low-mortality	DF	Sum Sq	Mean Sq	F value	P value
Days	1	2.064	2.064	315.723	< 0.001
Needle Type	1	0.0001	0.0001	0.018	0.895
Decomposer	1	0.069	0.069	10.507	0.005
Days x Needle Type	1	0.044	0.044	6.711	0.020
Days x Decomposer	1	0.323	0.322	49.348	< 0.001
Needle Type x Decomposer	1	0.027	0.027	4.054	0.061
Days x Needle Type x Decomposer	1	0.080	0.080	12.221	0.003
Residuals	16	0.105	0.001		

Table 2-6: Significantly dominant taxa in headwater streams across basins of varying levels of WbP mortality. Group 1 contains the streams in the high-mortality basin and Group 2 contains the streams in the low-mortality basin.

Taxon	Max Group	Observed IV	Mean IV from Monte Carlo test	SD of IV from Monte Carlo test	P value
Baetis bicaudatus	2	48.3	23.4	3.46	0.0002
Megarcys	2	37.3	13.1	2.91	0.0002
Paraleptophlebia	1	36.7	13.6	2.99	0.0002
Diamesa	2	36	11.6	2.79	0.0002
Prosimulium	2	34.8	18.2	3.43	0.0002
Baetis tricaudatus	1	30	11.6	2.78	0.0002
Paraleuctra	2	27.5	11.1	2.85	0.0002
Orthocladius	2	27.3	10.9	3.14	0.0002
Dipheter hageni	1	26.7	10.6	2.73	0.0002
Allomyia	2	26	9.1	2.67	0.0002
Panisopsis	2	25.8	11.3	2.98	0.0004
Doroneuria baumanni	1	23.3	9.4	2.54	0.0004
Zapada Oregonensis Gr.	1	18.3	8.2	2.61	0.0024
Micrasema bacro	1	15	6.7	2.17	0.0046
Rhyacophila Betteni Gr.	1	15	6.8	2.28	0.0064
Zapada columbiana	2	21.4	11.6	2.83	0.0074
Heterlimnius corpulentus	1	13.3	6.2	2.13	0.0086
Pagastia	1	23.3	13.4	3.2	0.0094
Rheotanytarsus	1	11.7	5.6	1.98	0.0118
Epeorus longimanus	1	11.7	5.7	2.09	0.0144
Ameletus	1	19.3	11.3	2.92	0.0184
Isoperla	1	13.4	7.3	2.23	0.0196
Visoka cataractae	2	11.2	5.8	2.13	0.0258
Zavrelimyia	1	10	5	1.87	0.0282
Oligochaeta	1	13.5	7.9	2.4	0.0304
Rhyacophila	1	10	5.2	2.01	0.0312
Ephemerella excrucians	1	10	5.3	2.02	0.0350
Rhyacophila narvae	1	12.7	7.5	2.46	0.0376
Krenosmittia	2	8	3.8	1.65	0.0432
Polycelis coronata	2	33.3	26	3.68	0.0446
Eukiefferiella	2	11.7	7	2.4	0.0468

FIGURES

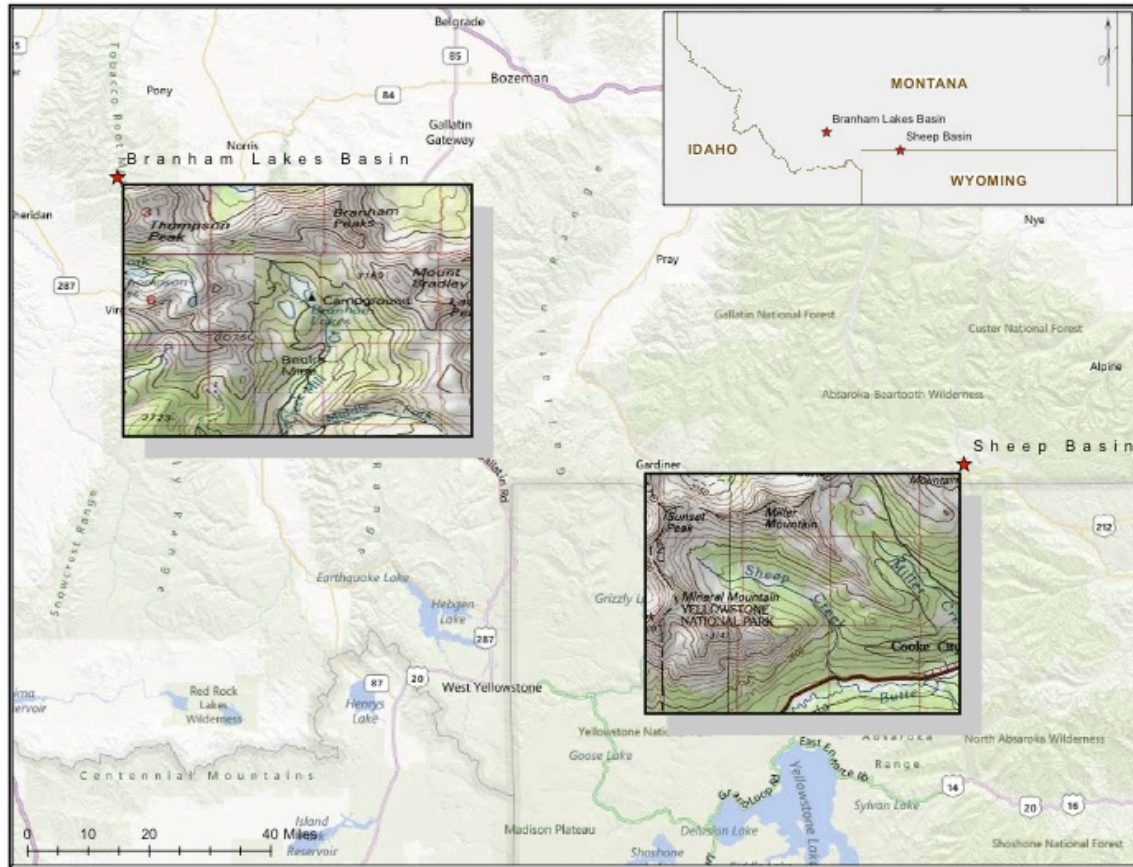


Figure 2-1. Location of study sites. This experiment took place in two streams. Mill Creek is located in Branham Lakes Basin, an area with very high levels of WbP mortality due to MPB. Sheep Creek is located in Sheep Basin, an area with relatively healthy WbP.

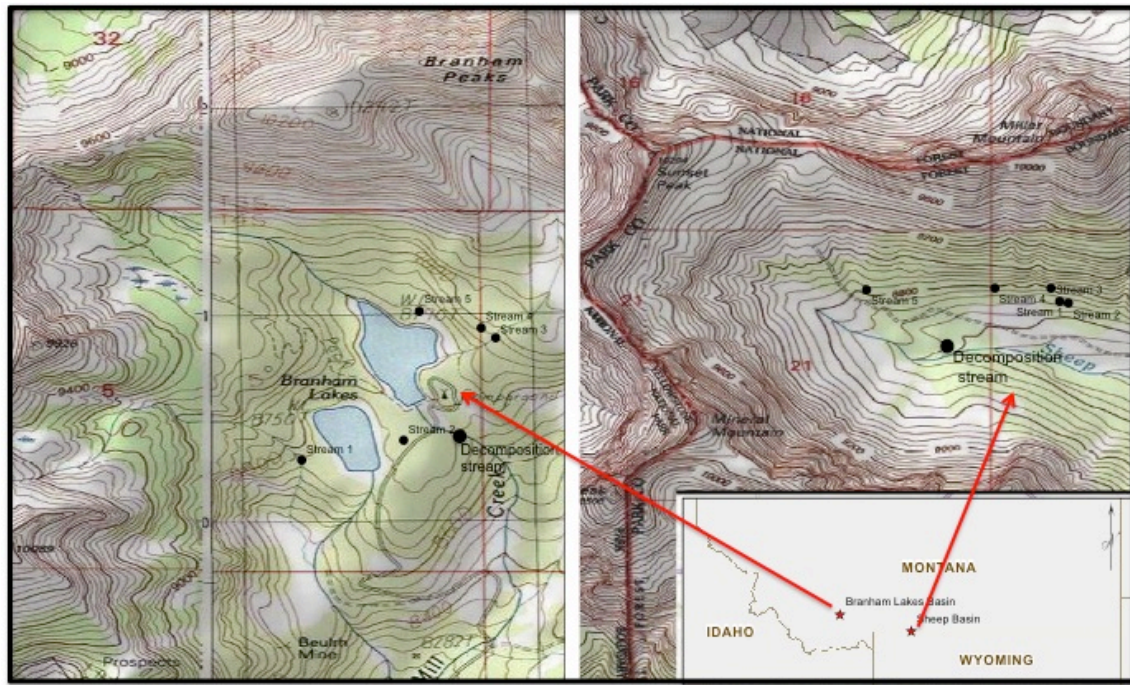
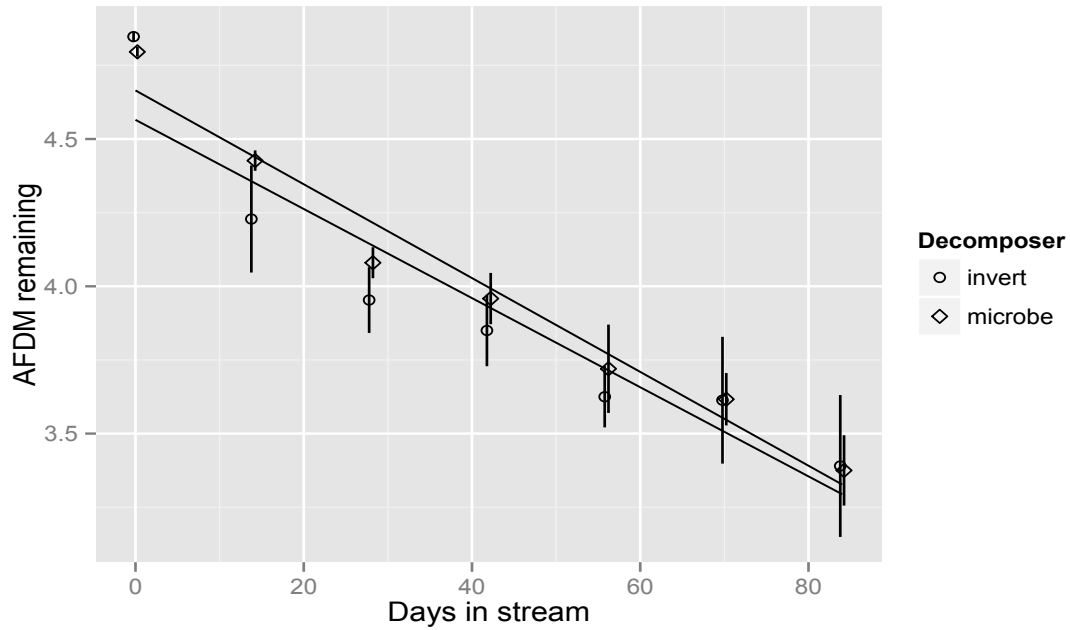


Figure 2-2: Locations of focal streams. WbP mortality is high in Branham Lakes basin and low in Sheep basin. Decomposition experiments took place in streams labeled “Decomposition stream” in each basin and benthic macroinvertebrate surveys were conducted in the six streams identified in each basin (streams 1-5 and the decomposition stream).

A.



B.

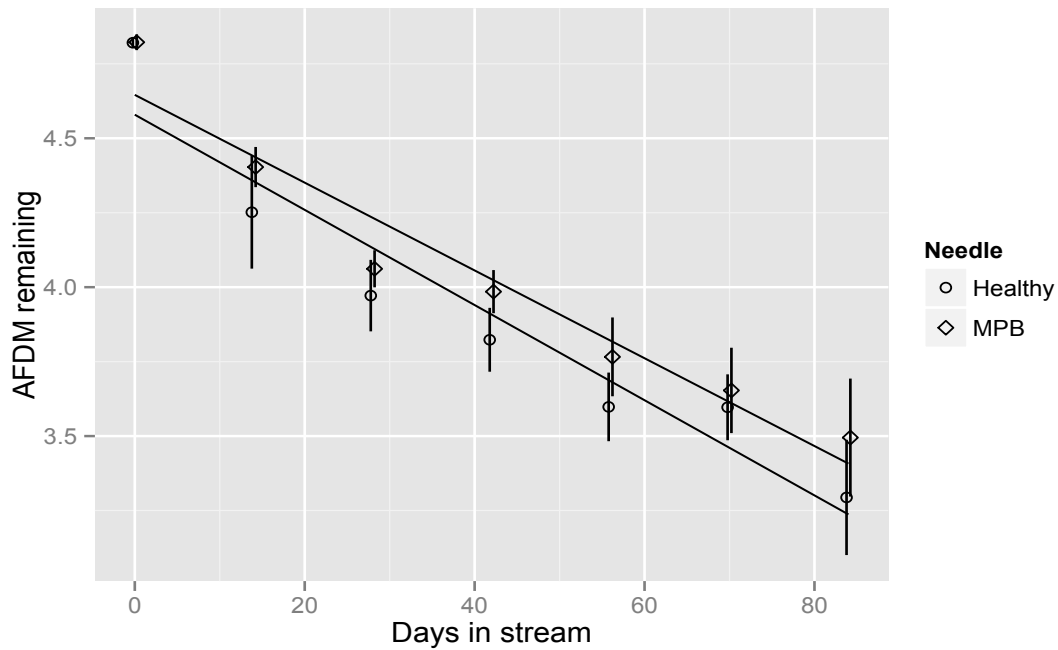
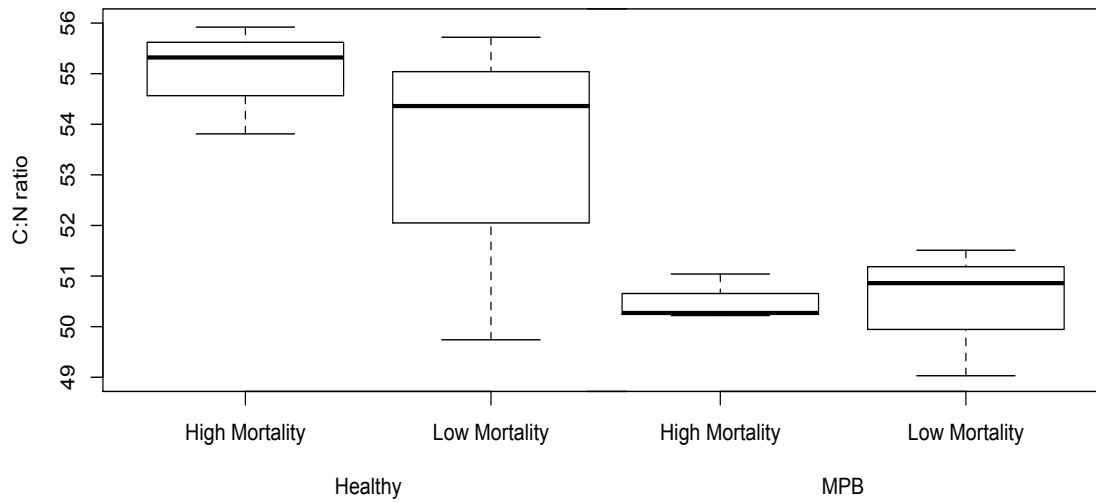


Figure 2-3. Trends in needle decomposition over time (means and 95% confidence intervals) with (A) grams AFDM remaining by needle type and (B) grams AFDM remaining by decomposer treatment. There is a general, albeit non-significant, trend in which healthy needles to decompose faster than MPB-altered needles. Likewise, there is a non-significant trend in which needles exposed to invertebrate consumers decompose faster.

A.



B.

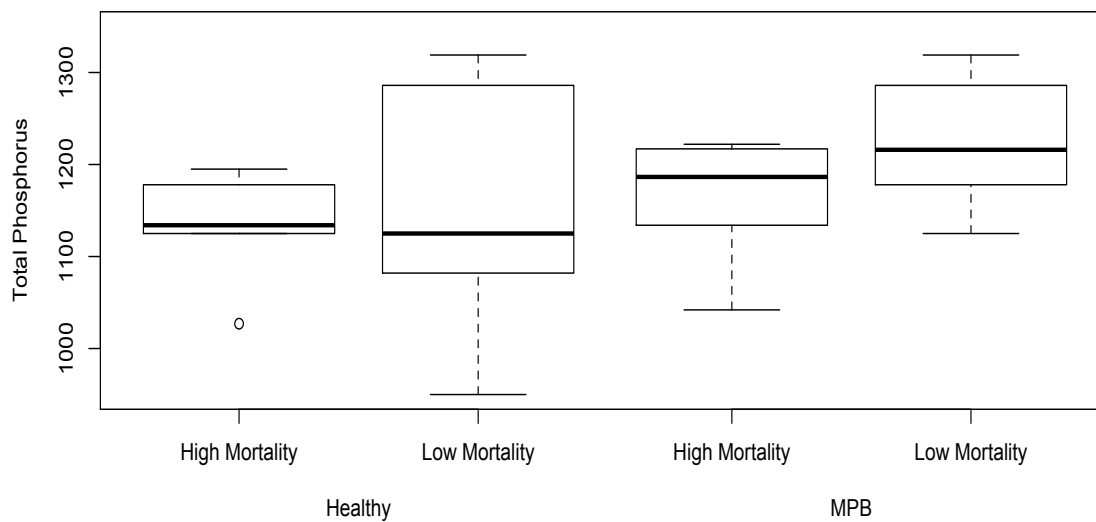


Figure 2-4: Litter quality for needles used in this decomposition study. Initial C:N values for (A) Initial C:N ratio (B) Total phosphorus at day 14.

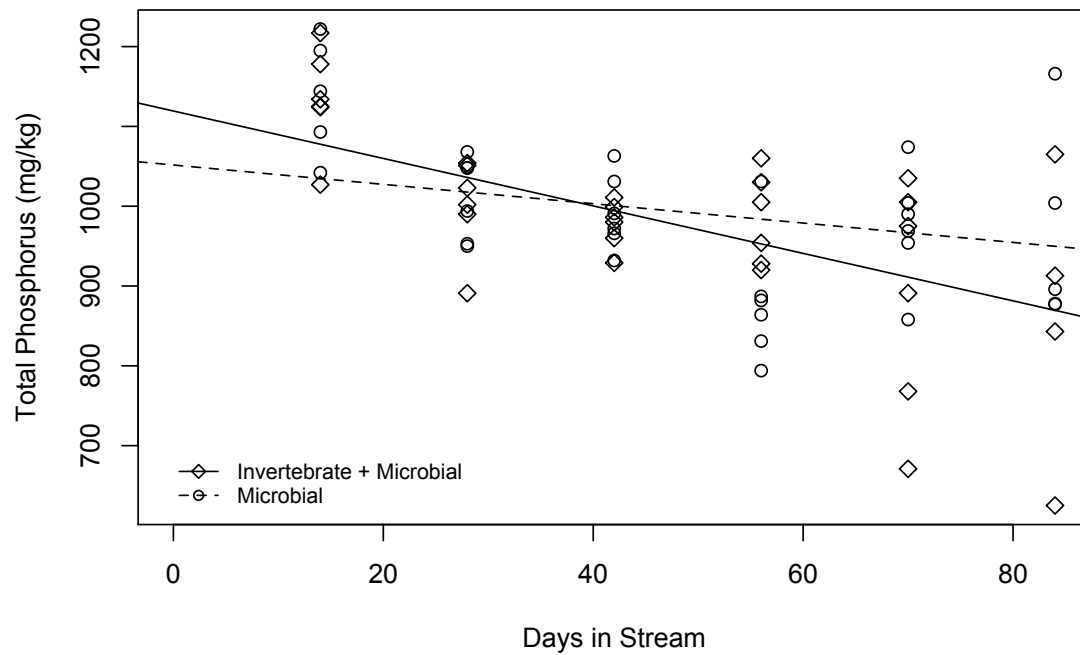


Figure 2-5: Total phosphorus in WbP needles over the course of the study. These data were collected from needles decomposing in the high-mortality stream.

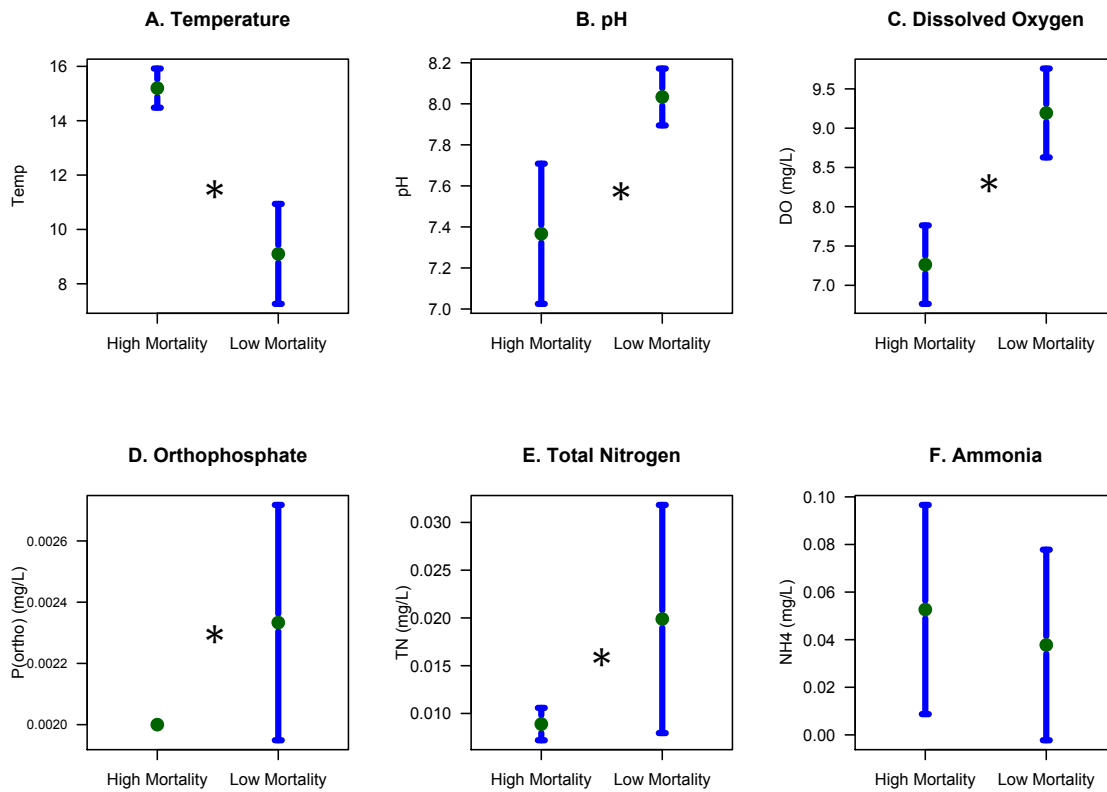


Figure 2-6: Stream chemistry parameters: (A) temperature (B) pH, (C) dissolved oxygen, (D) orthophosphate, (E) total nitrogen, and (F) ammonia. Each plot shows the mean with a 95% confidence interval for measurements of stream chemistry parameters and asterisks indicate significant differences. Sample sizes were different for the two streams: $n = 3$ for the low-mortality stream and $n = 6$ for the high-mortality stream.

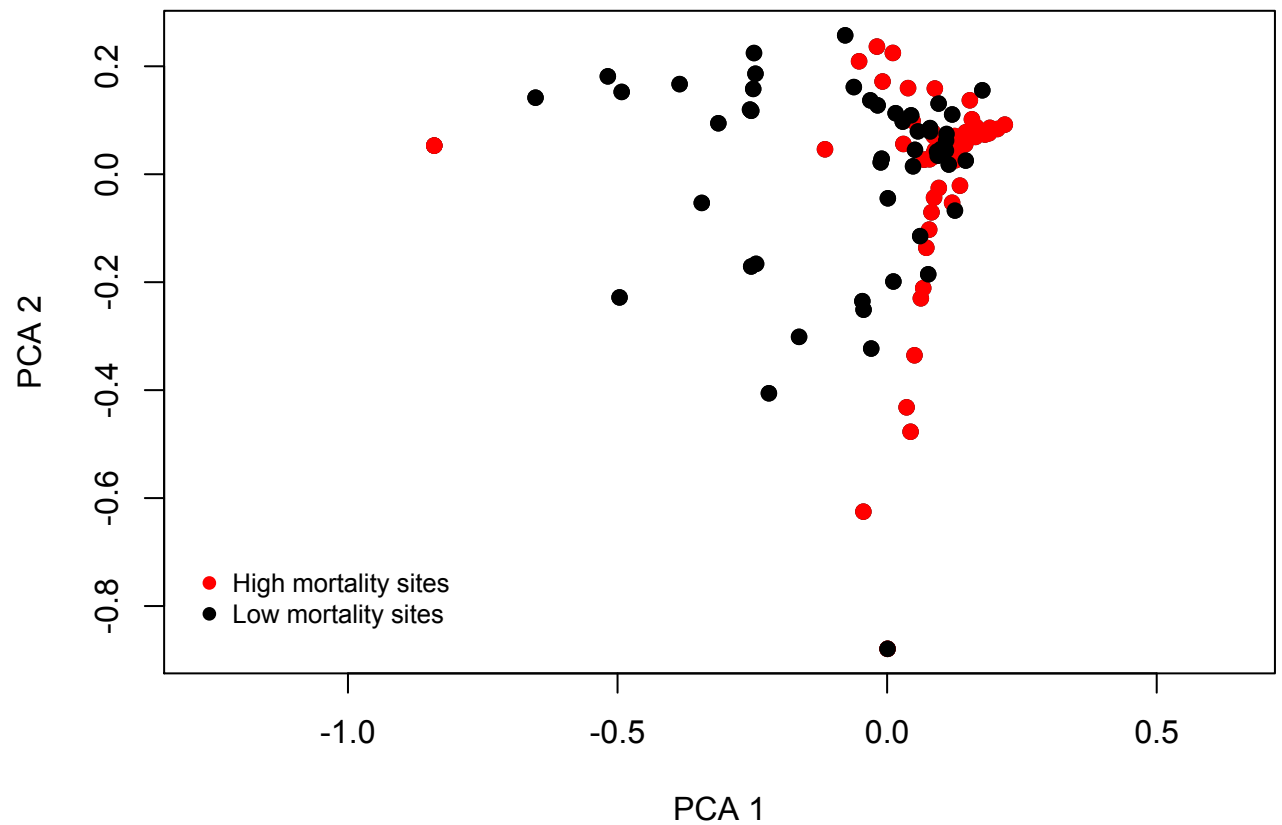


Figure 2-7: Results of principle components analysis of invertebrate taxa. The two treatment groups (high and low-mortality basins) are separated but weakly defined. Approximately 30% of the cumulative variance is explained between PCA 1 and PCA 2.

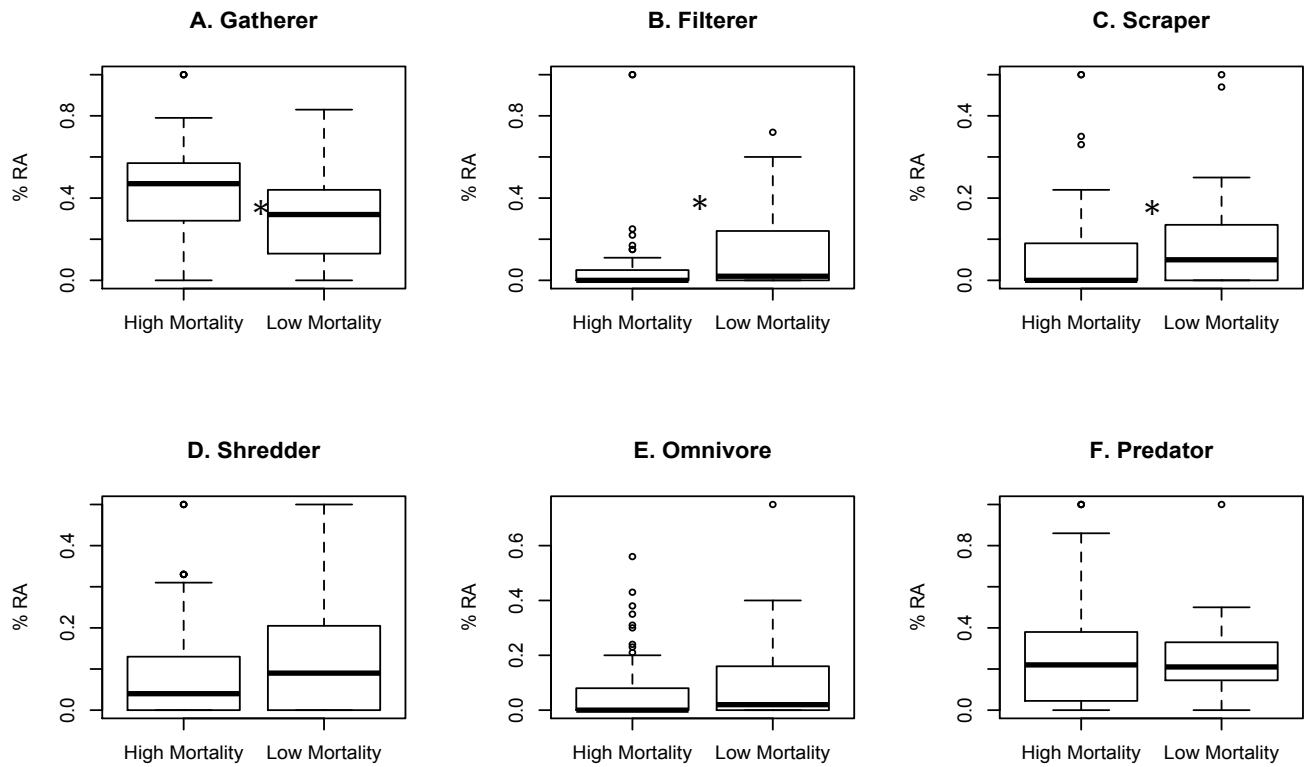
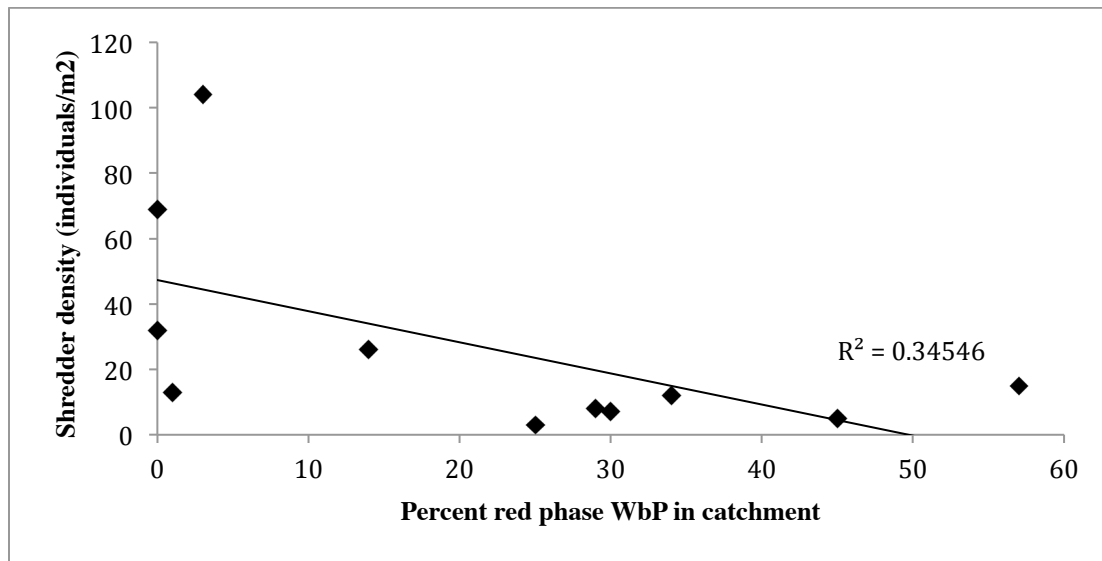


Figure 2-8: Differences in percent relative abundance of invertebrate functional feeding groups between basins: (A) collector-gatherers, (B) collector-filterers, (C) scrapers, (D) shredders, (E) omnivores, and (F) predators. Asterisks indicate significant differences.

A



B

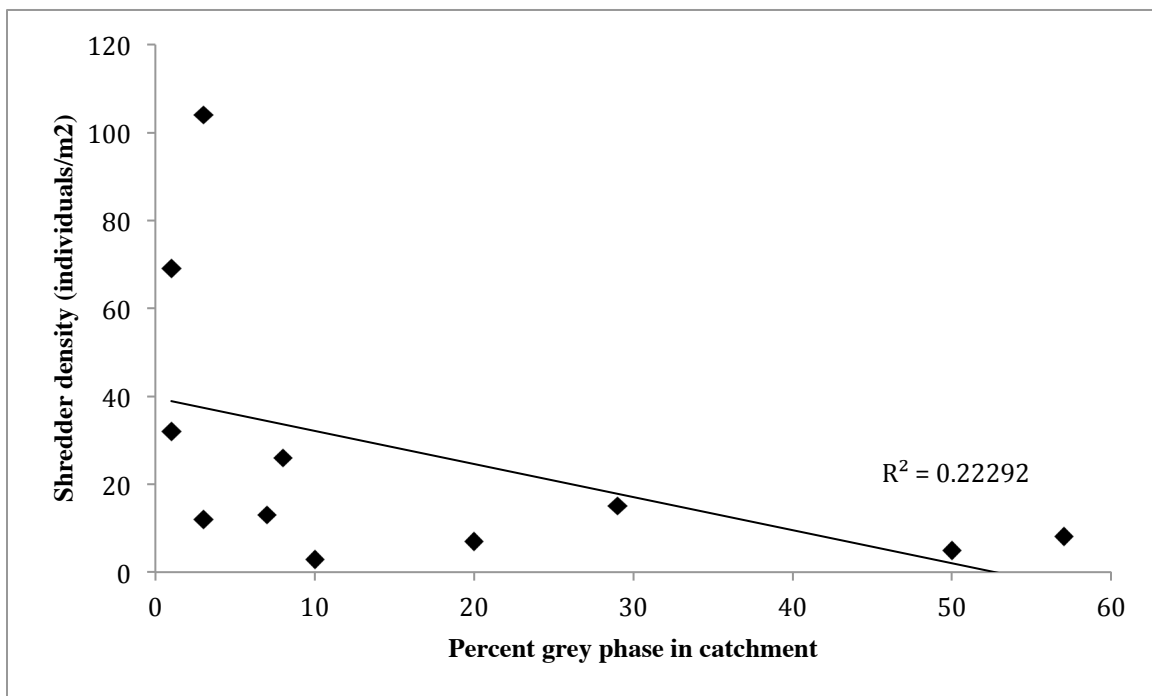


Figure 2-9. Mean density of shredding invertebrates decreases with (A) red phase mortality of whitebark pine and (B) grey phase mortality of whitebark pine.